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The Postcranial Skeleton of African Cynodonts

Farish A. Jenkins, Jr.

Bulletin 36

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Skeletal reconstruction of the cynodont *Thrinaxodon liorhinus,* approximately X1/2. This reconstruction is based primarily on the following specimens: axial skeleton, AMMM 5265; appendicular skeleton, SAM 1395; skull, USNM 22812 and other specimens (uncatalogued) belonging to the South African Museum.

The Postcranial Skeleton of African Cynodonts

Problems in the Early Evolution of the Mammalian Postcranial Skeleton

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THE POSTCRANIAL SKELETON OF AFRICAN CYNODONTS

Problems in the Early Evolution of the Mammalian Postcranial Skeleton

By Farish A. Jenkins, Jr.

ABSTRACT

Cynodonts are advanced mammal-like reptiles from which mammals probably were derived during Middle or Late Triassic times. The cynodont-mammal relationship, originally postulated primarily on the basis of cranial morphology, is here re-examined on evidence from postcranial anatomy. This study describes the postcranial skeleton of African cynodonts and offers functional interpretations with particular emphasis on posture and locomotion. *Cynognathus*, *Diademodon*, *Galesaurus* and *Thrinaxodon* are the principal genera studied; these and other cynodonts appear to have been very similar in their postcranial anatomy.

The cynodont atlas-axis complex, although basically reptilian in pattern, is incipiently specialized to permit atlanto-occipital flexion and extension as well as atlanto-axial rotation. Differentiation of the dens from the atlas centrum began in cynodonts and represents a functional replacement of the atlanto-axial zygapophyses lost to permit atlanto-axial rotation. The dens is not the homologue of the atlas centrum as is usually claimed on embryological evidence but is a neomorphic process of the atlas centrum.

During locomotion, the cynodont axial skeleton probably did not flex and extend in the sagittal plane as in mammals. Lateral undulation, typical of axial movement in reptiles, may have been facilitated in cynodonts by an enlarged iliocostalis system of muscles inserting on the costal plates. Functionally, the imbricating costal plates may be analogous to the expanded ribs in certain edentates and may represent part of a musculoskeletal adaptation to sustain a more characteristically "mammalian" posture with the trunk held persistently off the ground.

The cynodont glenoid was oriented posterolaterally and somewhat ventrally. The long axis of the humerus approximated a 45° angle to a parasagittal plane. Much of the propulsive force was transmitted directly to the scapula as in mammals. Propulsive movements of the humerus involved a significant amount of elevation and depression, thus presaging the movement typical of mammals. It is likely that some long axis rotation of the humerus, a primitive characteristic, was retained.

Like the forelimb and shoulder girdle, the cynodont hindlimb and pelvis possess a number of postural and morphological features that are advanced toward a mammalian condition. Among these are an obturator foramen of mammalian proportions, a socket-like acetabulum, and a bulbous, inflected humeral head. The femur was held

at angles of about 55° to a parasagittal plane. The mammalian lesser trochanter was derived from the reptilian trochanter internus by a slight shift in muscular insertion related to the repositioning of the limbs. In the cynodont foot a well-developed tuber calcis, sustentaculum tali, transverse tarsal arch and complex tarso-intermetatarsal articulations are all mammalian features. The pes, in one genus at least, was plantigrade and like the manus had the mammalian phalangeal formula of 2-3-3-3-3.

In details of morphology and function the postcranial skeleton of cynodonts should be regarded as neither "reptilian" nor "mammalian" but as transitional between the two classes. It is inappropriate to conceive of monotremes as representing a prototherian level of organization for in many ways monotremes are highly specialized.

ZUSAMMENFASSUNG

Die Cynodontier sind fortgeschrittene, den Säugetieren ähnliche Reptile, von welchen die Säugetiere wahrscheinlich während der mittleren oder späteren triassischen Zeit abstammten. Der Zusammenhang zwischen Cynodontier und Säugetieren, welcher ursprünglich hauptsächlich auf Grund der kranialen Morphologie postuliert wurde, wird hier erneut durch Befunde an der post-kranialen Anatomie untersucht. Diese Arbeit beschreibt das post-kraniale Skelett afrikanischer Cynodontier und bietet funktionsbedingte Auslegungen in welchen Haltung und Fortbewegen besonders berücksichtigt werden. *Cynognathus*, *Diademodon*, *Galesaurus* und *Thrinaxodon* sind die prinzipiellen Genera welche studiert wurden; diese und andere Cynodontier scheinen, in Bezug auf ihre post-kraniale Anatomie, sehr ähnlich gewesen zu sein.

Der Cynodontier Atlas-Achse Komplex, obwohl durchaus Reptile artig, zeigt eine anfängliche Spezialisierung um atlanto-occipitales Beugen und Strecken sowie atlanto-axiales Drehen zu erlauben. Die Differenzierung des Dens vom Atlas Zentrum begann in den Cynodontier und stellt einen funktionsbedingten Ersatz dar, für die atlanto-axiale Zygapophyse welche verloren war um eine atlanto-axiale Drehung zu ermöglichen. Der Dens ist kein Homolog des Atlas Zentrums als gewöhnlich behauptet auf Grund embryologischer Befunde, sondern ein neomorphischer Knochenfortsatz des Atlas Zentrums.

Im Fortbewegen hat das axiale Skelett der Cynodontier sich wahrscheinlich weder gebeugt noch gestreckt in einer sagittalen Ebene wie das der Säugetiere. Seitliche wellenförmige Bewegungen, die typische axiale Bewegungsweise der Reptile, könnten in Cynodontier erleichtert gewesen sein durch ein erweitertes ilio-costalisches Muskel System welches in den erweiterten Rippen eingeschoben war. Diese übereinanderliegenden erweiterten Rippen können den ausgedehnten Rippen mancher Edentaten entsprochen haben und eine muskulo-skelettale Anpassung vorstellen um eine mehr "Säugetier-artige" Stellung zu erhalten in welcher der Rumpf beharrlich oberhalb der Erde gehalten wurde.

Die Gelenkgrube des Schultergürtels der Cynodontier war posterolateral und etwas ventral orientiert. Der Winkel der langen Humerus-Achse betrug ungefähr 45 Grade zu einer parasagittalen Ebene. Ein grosser Teil der vorwärts treibenden Kraft wurde

wie in den Säugetieren direkt zur Scapula übertragen. Fortbewegungen des Humerus benötigten bedeutendes Erheben und Senken, in welchen die typischen Säugetier Bewegungen vorbedeutet sind. Wahrscheinlich wurde eine lange Achsendrehung des Humerus, ein primitiver Charakterzug, beibehalten.

Wie das Vorderbein und der Schultergürtel so besassen auch das Hinterbein und das Becken der Cynodontier einige morphologische Bildungen und eine körperliche Haltung die eine Annäherung an die Säugetiere zeigen. Das Obturator foramen hatte das Ausmass der Säugetiere, das Acetabulum war höhlenartig und der knollenartige Kopf hatte eine etwas seitlich gedrehte Haltung. Das Femur wurde in 55 gradigem Winkel zu einer parasigittalen Ebene gehalten. Das Trochanter minor der Säugetiere entstand vom Trochanter internus der Reptile durch eine geringe Veränderung einer Muskel Insertion im Zusammenhang mit der geänderten Stellung der Extremitäten. Zu diesen Zügen der Säugetiere zählen ein gut entwickeltes Tuber calcis, ein Sustentaculum tali, eine transverse tarsale Wölbung und komplizierte tarso-intermetatarsale Gliederungen im Fusse der Cynodontier. Zumindest eine Gattung hatte einen plantigraden Fuss, der, wie die Hand, die Phalangenformel von 2-3-3-3-3 der Säugetiere besass.

In den Details der Morphologie und Funktion sollte das post-kraniale Skelett der Cynodontier weder as "Reptile" noch als "Säugetier" artig betrachtet werden, sondern als ein Ubergang zwischen beiden Arten. Es ist nicht angebracht Monotremen als ein Exemplar einer Vorstuffe der Säugetiere anzusehen, da die Monotremen in vielen Beziehungen spezielle Bildungen besitzen.

РЕЗЮМЕ

К вопросу о заднечерепном скелете африканских цинодонтов и проблемы ранней эволюции заднечерепной анатомии млекопитающих

Цинодонты являются высокоразвитыми млекопитающеподобными пресмыкающимися к которым вероятно восходят млекопитающие. Это приурочивается к среднему и верхнему триасу. Взаимоотношение между цинодонтами и млекопитающими первоначально постулируется в первую очередь на основании черепной морфологии, пересматривается в настоящей работе с применением данных заднечерепной анатомии. В этом исследовании описывается заднечерепной скелет африканских цинодонтов и предлагаются функциональные истолкования, особенно подчёркивая положения тела и передвижение. Основными исследуемыми родами являются: *Cynognathus, Diademodon, Galesaurus, Thrinaxodon.* У этих цинодонтов, как и у других, выявляются существенные сходства по заднечерепной анатомии.

Хотя атлантоаксиальный комплекс цинодонтов в основных своих чертах соответствует модели пресмыкающихся, но является зачаточно-специализированным, чтобы позволить атланто-затылочное сгибание и растягивание как и атлантоаксиальное вращение. Дифференциация между зубовидным отростком и телом атлантового позвонка возникла первоначально у цинодонтов и представляет функциональное замещение атлантоаксиального сочленовного отростка в результате исчезновения которого стало возможным атлантоаксиальное вращение. Зубовидный отросток не является гомологом тела атлантового позвонка как обычно утверждают на основании эмбриологических данных, а являются его неоморфным процессом.

Во время передвижения, аксиальный скелет цинодонта вероятно не сгибался и не растягивался в сагиттальной плоскости подобно млекопитающим. Возможно что боковой ундулеции, которой характеризуется аксиальное движение пресмыкающихся, способствовала у цинодонтов увеличенная подвздошно-реберная мышечная система прикрепляющаяся к реберным пластинкам. С функциональной точки зрения, возможно что черепитчаторасположенные реберные пластинки аналогичны расширенным ребрам у определенных эдентатов и представляют часть скелетно-мышечной адаптации целью которой является более характерная "млекопитающим" способ держать тело с постоянно приподнятым туловищем.

Суставная впадина лопатки у цинодонтов была постеролатерально и до некоторой степени вентрально направлена. Угол продольной оси плечевой кости к парасагиттальной плоскости равнялся приблизительно 45 градусам. Значительная часть пропульсивной силы передавалась прямо на лопатки, подобно млекопитающим. Пропульсивные движения плечевой кости сопровождали значительное суммарное движение вверх и вниз, таким образом предвещая движения характеризующие млекопитающих. По всей вероятности сохранилось определенное вращение продольной оси плечевой кости, являющееся примитивной чертой.

Как передние конечности и плечевой пояс, так и задние конечности и таз у цинодонтов обладают несколькими свойствами относящимися к морфологии и к способу держать тело, развивавшимися в направлении к млекопитающим. Среди этих черт следует отметить запирательное отверстие соответстующее пропорциям у млекопитающих, впадиноподобное *acetabulum*, луковицеобразная, вогнутая плечевая головка. Бедро держалось приблизительно под углом 55 градусов к парасагиттальной плоскости. Малый вертлюг у млекопитающих восходит к рептильному внутреннему вертлюгу, с небольшим смещением мышечного прикрепления относящегося к переставлению конечностей. Стопа ноги у цинодонта характеризуется следующими чертами млекопитающих: хорошо развитый бугор пяточной кости, поддерживающий надпяточную кость; поперечная предплюсневая дуга; и комплексные предплюснемежплюсневые суставы. Нога, по крайней мере у одного рода, была стопоходящей и подобно руке имела суставную формулу пальцев млекопитающих (2-3-3-3-3).

Что касается подробностей морфологии и функции, заднечерепной скелет у цинодонтов не следует считать ни "рептильным", ни относящимся к "млекопитающим", а переходным между двумя классами. Неуместно предполагать, что цинодонты достигли уровня организации соответствующего яйцекладущим млекопитающим, ибо во многих отношениях однопроходные являются высокоспециализированными животными.

INTRODUCTION

The evolutionary emergence of the Class Mammalia involved a period of transition some 100 million years long. During this time, mammalian forebears gradually acquired much of the basic structure which now characterizes living members of the class. But the transition between the earliest synapsids and the earliest therians is represented by an obviously incomplete fossil record. Despite its incompleteness, however, a great diversity of transitional forms is known. Cynodonts represent one of the most advanced groups of reptiles which manifest many mammal-like features. In the cynodont skull, for example, features which represent or otherwise anticipate the mammalian pattern are the double occipital condyles, the secondary palate, the ethmoturbinals and the proportionately large dentary bone. African cynodonts were small to medium-sized animals, varying in length from approximately 35 cm (*Thrinaxodon*) to as much as 150 cm or more (*Cynognathus*). The cynodont dentition underwent rapid evolutionary change, partly the result of dietary specialization but also in conjunction with musculoskeletal changes in the lower jaw. Traversodontids and diademodontids undoubtedly were herbivorous; procynosuchids and galesaurids were probably insectivorous and carnivorous, while most cynognathids were strictly carnivorous. The taxonomic interrelationships of cynodonts and related forms constitutes a significant problem in itself, and complicates the search for the origin of mammalian anatomical features. In this study no attempt is made to solve questions as to the origin or interrelations of cynodonts, the solution to which must come from studies on cranial morphology (see Watson and Romer, 1956; Romer, 1969b).

The scope of the present survey is restricted to African cynodonts. Earlier research on South American cynodonts (von Huene, 1935–1942; 1944–1948; Cabrera, 1943) is now being supplemented and expanded by Bonaparte (1962–1966e and later papers) and Romer (1966, 1969a, 1969b). I have recently described the postcranial skeleton of a new traversodontid from Argentina (Jenkins, 1970a) but aside from this study have not had the opportunity to examine other South American material. For this reason I make only limited reference to South American cynodonts and base my conclusions primarily on the excellent papers of Bonaparte. Of the Russian forms, only a description of the postcranial skeleton of *Permocynodon* (Konjukova, 1946) is available.

The present study on the postcranial skeleton of African cynodonts has a dual purpose: first, to provide an adequate morphological basis for comparison with postcrania in other therapsids and in early mammals, and second, to evaluate the cynodont postcranial skeleton as a possible stage in the evolution of mammalian features.

No comparative survey of the cynodont postcranial skeleton has even been published nor has the role of cynodonts in the evolution of mammals been universally acknowledged. Both of these facts are best understood in their historical context which now will be briefly summarized.

In 1844, Sir Richard Owen described the first mammal-like reptile (*Dicynodon*) from cranial material collected by A. G. Bain some years earlier. Owen compared the cranial features of this fossil to various orders of reptiles, concluding that "the general type of cranial organization manifested by modern lizards was that in which the peculiar modifications of the *Dicynodon* have been superinduced." Only the long tusks gave Owen any reason to make reference to mammals. Citing seemingly appropriate analogies with mammalian tusks and canine teeth, he added that *Dicynodon* manifested a "much more important step towards the mammalian type of dentition by maintaining the serviceable state of the tusk by virtue of constant renovation . . . according to the principle manifested in the long-lived and ever-growing tusks and scalpriform incisors of the Mammalia." This was, for Owen, the only implication of mammalian affinities of *Dicynodon*, and obviously he regarded it as a peculiarity of no phylogenetic importance.

For the three decades following Owen's original description, papers by Owen and others on mammal-like reptiles were devoted primarily to describing morphological aspects of the cranium, with little attention paid to the postcranial skeleton. In general, these papers disclosed a general lack of appreciation of the mammal-like features and affinities of therapsids. Within the context of mid-nineteenth century paleontology, it is even surprising that the evolutionary status of Karroo fossils was recognized as soon as it was. As early as 1861 Owen wrote that *Galesaurus planiceps* possesses "that remarkable resemblance to the mammalian carnivorous dentition, which has led to a foundation of a family [Cynodontia] for its reception in the group of reptiles characterized by the anomalous departures from the type of dentition in the great Saurian order of Cuvier." Yet the many reptilian features of these fossils, and the fact that Huxley and others maintained that mammals arose directly from Amphibia, delayed recognition that therapsids were the stock from which mammals arose.

Owen's monographic *Catalogue of the Fossil Reptilia of South Africa* (1876) contains several allusions to the mammal-like features of theriodonts and anomodonts. Most of the comparisons, however, were made with dinosaurs and living reptiles. Evidently Owen could not bring himself to accept the possibility that among them were the reptilian ancestors of mammals. Of the mammal-like features of anomodonts and theriodonts he concluded: "Certain it is that the lost reptilian structures specified in the present Catalogue are now manifested by quadrupeds with a higher condition of cerebral, circulatory, respiratory and tegumentary systems [i.e., mammals] —a condition the acquisition of which is unintelligible to the writer on either the Lamarckian or Darwinian hypothesis."

In November, 1878, E. D. Cope read a paper before the National Academy of Sciences in which he proposed the Pelycosauria and Anomodontia (including all South African therapsids then known) as Suborders of the Order Theromorpha. This order he "regarded . . . as approximating the Mammalia more closely than any other division of Reptilia, and as probably the ancestral group from which the latter were derived" (Cope, 1878: 829–830). The misuse of the word "latter" muddles Cope's

intended meaning. Cope's remarks were transcribed and probably not reviewed by him prior to the issue of the *Proceedings*. In any event, it is clear from the context that Cope proposed that mammals, not reptiles, arose from the Theromorpha. This marks one of the earliest positive statements on the reptilian ancestry of mammals. Owen speculated along similar lines in 1880, suggesting that monotremes might be derived from Karroo Triassic reptiles.

Paleontologists of the last two decades of the nineteenth century were fully occupied with descriptive studies of an abundance and diversity of Permo-Triassic vertebrates. A minor polemic over a suitable classification occupied Cope and H. G. Seeley; both of these authors, although cognizant of the pre-mammalian status of therapsids, did little to advance the investigation of mammal origins. In 1888 Seeley concluded, with reference to *Pareiasaurus* and allied genera, that their "mammalian structures have been transmitted to mammals, if not in direct line, which is improbable, by collateral derivation from a common ancestry." Ten years later, at a meeting of the International Congress of Zoology, the origin of mammals was discussed by Seeley, H. F. Osborn, O. C. Marsh, Haeckel and others (Seeley, et al., 1898: 69–76). Seeley acknowledged that theriodonts could be regarded as mammalian ancestors, but cited so much apparently conflicting evidence that the matter could not be conclusively settled. He concluded that "anomodonts [which to Seeley meant anomodonts *sensu stricto* plus theriodonts] are not the ancestors of mammals, but a collateral and closely related group. The common parent of both may be sought in rocks older than the Permian, perhaps in Silurian and Devonian strata." Osborn agreed with Seeley's view that no known therapsid could be a mammalian ancestor. But he suggested, instead, that a then unknown group of "anomodonts" (*sensu latu*) gave rise to mammals, and that many mammalian characters shared by known "anomodonts" and mammals were the result of independent, parallel acquisition. Marsh cited the fact that known mammals were so diverse as to leave "an open question whether all have a common origin"—thereby introducing the question of polyphyly. Marsh favored the Huxleyian theory of mammalian derivation directly from amphibians. Thus, at the turn of the century, the question of the origin of mammals was largely unresolved.

The development of viable theories of mammalian origins, as well as the understanding of relationships within the Therapsida, is largely the work of Robert Broom and D. M. S. Watson. As early as 1901, Broom hypothesized that mammals arose from primitive theriodonts, on or near the stem which gave rise to *Cynognathus* and *Diademodon*. In 1905, he specifically included cynodonts in the mammalian lineage, and repeated this opinion (Broom, 1907, 1913a, 1915) as better material became known. At about the same time Watson (1913) thought that a "pre-therocephalian" was the common ancestor of therocephalians, cynodonts and mammals. Shortly thereafter he changed his opinion, stating that the Suborder Gorgonopsia gave rise to mammals (Watson, 1917b). The discovery of ictidosaurs re-emphasized the mammal-like characters of cynodonts and Broom advocated that mammals were derived from ictidosaurs and these, in turn, arose from cynodonts (Broom, 1929). Later, Broom (1932b) reaffirmed his opinion that mammals originated from ictidosaurs but expressed uncertainty over ictidosaur origins, inclining to the belief that ictidosaurs evolved from "a small primitive Bauriamorph" rather than "a small primitive cynodont".

Despite Broom's last and somewhat equivocal opinion on cynodont-ictidosaur relationships, there is little doubt that the cynodont skull possesses numerous mammalian features (as demonstrated by Broom, Watson, Brink and others). Recent work has brought forward additional evidence for a cynodont-mammal relationship (see Hopson and Crompton, 1969). Brink (1967), however, still prefers the alternate hypothesis that mammals arose from a bauriamorph (*sensu* Watson and Romer, 1956) although this relationship is not supported by any recent morphological analysis. The hypothesis of a bauriamorph-mammal relationship probably derives from Broom's (1909) original description of *Bauria* as a primitive cynodont rather than as a representative of a new infraorder, the Bauriamorpha. For some time, at least, Broom (1929: 690) "was inclined to find the mammalian ancestor in one of the Bauriamorphs". But aside from a few incidental references to the secondary palate and other advanced features, no worker has since been able to establish that bauriamorphs are more likely to have been mammalian ancestors than cynodonts. Yet the hypothesis persists. For example, Crompton (1955a, 1958) concluded that the ictidosaur *Diarthrognathus* could not have been derived from any known cynodont and suggested that it was derived from bauriamorphs. Thus Brink (1956), following Crompton, diagrammatically represented the line of mammalian evolution passing from *Scaloposaurus*, close to *Bauria*, through the ictidosaurs to mammals. However, Kermack (1967) and Crompton (*in* Crompton and Jenkins, 1968) now believe that ictidosaurs represent advanced but somewhat aberrant cynodonts and have no part in mammalian ancestry (a view expressed by von Huene in 1940). Thus the theory of a bauriamorph origin for mammals as advocated by Brink appears to be even less tenable. At the present time Triassic mammals are becoming better known and cynodonts are favored as percursors of some, if not all, of Triassic groups of mammals on the basis of cranial structure and dentition (Hopson, 1964, 1967; Crompton and Jenkins, 1968; Hopson and Crompton, 1969).

The history of studies on cynodont postcrania is short. Owen (1876: 21, Pl. XIX) briefly described the coracoids and parts of a left humerus of *Cynochampsa laniarius* (considered questionably synonymous with *Diademodon* by Watson and Romer, 1956: 65). This material, which could not be located for re-examination, probably represents a cynodont and was thus the first cynodont postcranial remains to be described. Subsequent to Seeley's (1895a, 1895b) monographs on *Cynognathus* and other genera, descriptions of cynodont postcranial material were usually incidental to discussions of cranial morphology. Broom, Broili and Schröder, Crompton, Haughton, Parrington, von Huene and Watson all described various aspects of incomplete and sometimes generically indeterminate postcrania. More recently, Brink and Kitching have published the most comprehensive accounts of African cynodont postcrania since Seeley's papers.

Without detracting from the contributions of the aforementioned authors, it should be noted that the available cynodont material was and still is, in quantity and quality, much less than might be desired for so important a group. To some extent the present study suffers from these inadequacies. However, this disadvantage is partially offset by new material as well as by the fact that the major differences between cynodont genera are in cranial morphology. The postcranial skeletons, insofar as known, are remarkably alike. Thus it is possible to present a reasonably accurate portrayal of

"the cynodont" postcranial skeleton despite the lack of a complete and well-preserved skeleton for any given genus.

Cynodont species distinctions are so inadequately established in terms of modern systematic technique that with few exceptions the genus is the practical taxonomic unit used by most workers. Lack of samples sufficient to permit statistical evaluation is principally responsible, for many species appear to have been named without extensive comparative study. Pending a major systematic revision, trivial names are deemed unreliable. Species designations are therefore largely neglected in this study and the genus is substituted as the working taxonomic unit. This approach is also justified on the basis of the great similarity among cynodont postcranial skeletons. Among all the available postcranial materials possibly representing two or more species of the same genus, no differences could be detected that might indicate species diversity.

For each element of the postcranial skeleton discussed, an introductory section on material briefly summarizes what is available for study and which previous studies are applicable. Material cited specifically by museum or collection number is material that I have examined personally; the only exception is the type of *Leavachia duvenhagei* (RC 92), for which I had a complete series of stereoscopic photographs. Each succeeding section on morphology is a summary and comparative description of representative material. Ideally, a description of the postcranial skeleton is most informative when related to other anatomical features, especially muscles. In some cases, e.g., the humerus and femur, the comparative anatomy is sufficiently well known to permit reasonably confident reference to the muscles associated with various features. In other cases, where the disposition of muscles is in doubt, the description is necessarily strictly morphological. Following the descriptive sections, discussions of selected functional problems are appended.

I have been obliged to follow zoological (rather than anatomical) usage with regard to spelling, capitalization, etc., of anatomical terms.

Abbreviations

AMMM — Alexander McGregor Memorial Museum, Kimberley, R.S.A.
AMNH — American Museum of Natural History, New York
BMNH — British Museum (Natural History), London
BPI — Bernard Price Institute for Palaeontological Research, Johannesburg, R.S.A.
DMSW — D.M.S. Watson Collection, now housed in the University Museum of Zoology, Cambridge, England
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
NMB — National Museum, Bloemfontein, R.S.A.
RC — Rubidge Collection, privately owned by the Rubidge family, Graaff-Reinet, R.S.A.
SAM — South African Museum (Natural History), Cape Town, R.S.A.
TM — Transvaal Museum, Pretoria, R.S.A.
UCMP — University of California Museum of Paleontology, Berkeley
UMC — University Museum of Zoology, Cambridge, England
YPM — Peabody Museum of Natural History, Yale University, New Haven, Connecticut: Vertebrate Paleontology Collection
YPMOC — Peabody Museum of Natural History: Osteology Collection

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Drs. John H. Ostrom and Edmund S. Crelin of the Departments of Geology and Anatomy, respectively, Yale University, read the manuscript in its entirety and offered criticisms that substantially improved the text. Dr. G. E. Erikson of the Division of Biological and Medical Sciences, Brown University, constructively reviewed certain aspects of the text. Dr. Robert Shapiro, Chief, Department of Radiology, Hospital of St. Raphael, New Haven, provided a critique of my discussion of the atlas-axis complex. To all of the above I express my gratitude for their participation in this study. However, I alone am responsible for any errors or faulty interpretations that might appear.

This study could not have been completed without the helpful cooperation from the staff of many museums and research institutions. In particular I would like to acknowledge: Dr. F. R. Parrington, F.R.S., for the loan of numerous specimens from the Cambridge University Museum of Zoology and from the collection of Professor D. M. S. Watson (now housed in that museum); Dr. J. W. Kitching, of The Bernard Price Institute for Palaeontological Research, Johannesburg, for the free use of that institute's facilities and collection of cynodonts; the late Dr. A. C. Hoffman, Director of the National Museum, Bloemfontein, for permission to study and to cast important specimens in his care; Dr. T. H. Barry, Director of the South African Museum (Natural History), Cape Town, for the use of museum facilities and for permission to study the collection of cynodonts; and Dr. A. J. Charig, of the British Museum of Natural History, for access to important type material in his department.

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The illustrations in this paper are either directly or indirectly due to the artistic skills of Carl R. Wester, Jr., of the Peabody Museum of Natural History. I am most indebted to him for preparing Figures 12, 17, 22, 24, 26, 27, 29, 31, 35, 44, 47, 48, 56, 58 and 61, and for having patience in teaching me skills sufficient to execute almost all of the remaining figures myself. His substantial contribution to this work is gratefully acknowledged. Robert J. Demarest executed the frontispiece and Robert Bakker aided in rendering Figures 5, 8, 19, 20, 40 and 42.

A. H. Coleman took the stereoscopic photographs in Figure 38, and Charles R. Schaff contributed his skills in many preparational tasks. The sagittal section of the atlas-axis complex of a 20-day-old *Didelphis marsupialis* (Fig. 9) was kindly loaned by the Wistar Institute of Philadelphia. Dr. Edmund S. Crelin of the Department of Anatomy, Yale University, provided the facilities and Elmer Newton the technical assistance that made possible the sectioning of a 25-day-old *D. marsupialis.* Louise Holtzinger and Irene Walter typed the entire manuscript at various stages in its preparation. To all of the above I am most grateful.

This study was submitted as a dissertation in 1968 to the faculty of the Graduate School of Yale University in candidacy for the degree of Doctor of Philosophy. Since that time it has been possible to make certain changes and additions, and I thank Professor Edward W. Dempsey, Chairman of the Department of Anatomy, Columbia University, for providing me with the necessary facilities. This Bulletin has been published with the aid of a National Science Foundation Publication Grant, No. GN–528.

PART ONE. POSTCRANIAL AXIAL SKELETON

1. ATLAS-AXIS COMPLEX

MATERIAL. The atlas and axis of the type of *Thrinaxodon liorhinus* (BMNH R.511) are excellently preserved and nearly complete except for the first intercentrum and portions of the arch. Incomplete atlas elements are preserved with other specimens of *T. liorhinus* (BMNH R.511a, BMNH R.3731, AMMM 5265, USNM 22812). Broom (1932b: 270) gave a diagrammatic figure of an atlas of *Thrinaxodon.*

The atlas-axis complex of *Galesaurus planiceps* is known from a specimen (UMC R.2721) described by Parrington (1934). This specimen, which subsequently has been fully prepared in acid, is one of the very few cynodonts for which the paired proatlas plates are known.

The type specimen of *Cynognathus crateronotus* (BMNH R.2571) preserves only the axis with the fused atlas centrum.

Brink (1955: 23–24) figured and described a cynodont axis (DMSW R.205) and an atlas neural arch (DMSW R. 202). He implied that these were from *Diademodon* (his paper being a study of *Diademodon*) but he never actually identified the specimens as such. In fact, the specimens are not listed in the D. M. S. Watson catalogue as positively associated with diagnostic cranial material, and therefore they must be considered generically indeterminate.[1] Kühne (1955: 99) also figured and described DMSW R.202 as *Diademodon* sp. The orientations of the arch as figured are incorrect (compare his fig. 41 with my Fig. 4).

Atlas elements positively referable to *Diademodon* are associated with a skull, the lower jaw of which was originally described as *Gomphognathus* by Janensch (1952: 237). A cast of the articulated right atlas arch and proatlas was available for study. In addition, Broom (1903) gave a complete description, including excellent figures, of both *Gomphognathus* (= *Diademodon*) *kannemeyeri* and *Trirachodon kannemeyeri.* Both of these specimens possess proatlas ossicles.

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[1] The D. M. S. Watson collection catalogue records the following information: "Collected from a small bone bed at the base of the hill immediately opposite the police station at Lady Frere. Nos. R.131–R.226 collected there, all *Diademodon*, but several spp. of different sizes may be present." However, in at least several other localities, "bone beds" containing disarticulated *Diademodon* remains also contain *Cynognathus* remains. Although Watson claimed that only *Diademodon* was represented, this fact cannot be verified because 1) the skeletal elements were disarticulated and 2) *Diademodon* cannot be distinguished as yet from other large cynodonts on the basis of postcranial anatomy.

A collection of *Cynognathus* and *Diademodon* (BPI 1675) disarticulated postcranial skeletons contains isolated and incomplete atlas-axis elements, including what is apparently the first intercentrum. In this small sample, no morphological differences could be discerned by which the two genera might be distinguished. Except for size, the atlas-axis complex of these larger cynodonts is very similar to those of *Thrinaxodon* and *Galesaurus.*

Broili and Schröder (1936: 61–63) described an axis with a fused atlas centrum, which, on the basis of associated cervical vertebrae and a cranial fragment, they believed to represent *Cynognathus platyceps.* A cast of this specimen was available for study.

Atlas

MORPHOLOGY. The cynodont atlas consists of four separate ossifications: a centrum, two halves of the neural arch, and the first intercentrum. Broom (1903) incorrectly implied that cynodonts lack an atlas centrum; he refers to the actual atlas centrum as an "odontoid process", apparently regarding this as a derivative of the axis or second vertebra. The centrum in galesaurids (Figs. 1G, 2A, 3B) is slightly shorter anteroposteriorly than those of other cervicals; in *Thrinaxodon liorhinus* (BMNH R.511) the lengths of the atlantal and axial centra are 3.7 mm and 8 mm respectively, while in *Galesaurus planiceps* (UMC R.2721) the lengths are 6.5 mm and 8 mm respectively. The overall smaller size of the atlas centrum in *Thrinaxodon* may be partly the result of post-mortem distortion but probably also reflects some measure of actual size disparity. The anterior surface bears a large convex articular facet which is divisible functionally into four areas (Fig. 2B). The first two comprise the dorsolateral wings of the facet (*f at a*) extending posteriorly on each side and almost reaching the bases of the axis pedicles. These areas face dorsolaterally as well as anteriorly and articulate with a cup-shaped facet on each half of the atlas neural arch. The third area (*f a i*) projects ventrally and faces anteriorly and slightly ventrally; it articulates with a broad, shallowly concave facet on the posterodorsal surface of the first intercentrum. In *Cynognathus* this area is more ventrally oriented than in smaller cynodonts (Broili and Schröder, 1936). Directly above lies the fourth area which is broadly convex transversely and faces for the most part anteriorly. In some but not all specimens a faint, median swelling or tubercle occurs adjacent to the dorsal rim (*d*, Figs. 2A, B, 3C, D); the possible significance of this structure is discussed below in reference to the evolution of the dens. The tubercle and surrounding area incompletely divides the atlanto-occipital joint into separate articular areas for the incipiently differentiated occipital condyles.

The dorsal surface of the atlas centrum bears a broad, oval concavity, the surface of which is perforated by two or more nutrient foramina (*nu f*, Fig. 1G). The surface is confluent with that on the dorsal surface of the axis centrum and represents the floor of the neural canal.

The posterior face of the atlas centrum appears to be fused to the axis centrum in the types of *Thrinaxodon liorhinus* (BMNH R.511) and *Cynognathus crateronotus* (BMNH R.2571). It is difficult to be certain of the condition in the latter because of the presence of indurated matrix joining all cervical vertebrae. However, in one specimen

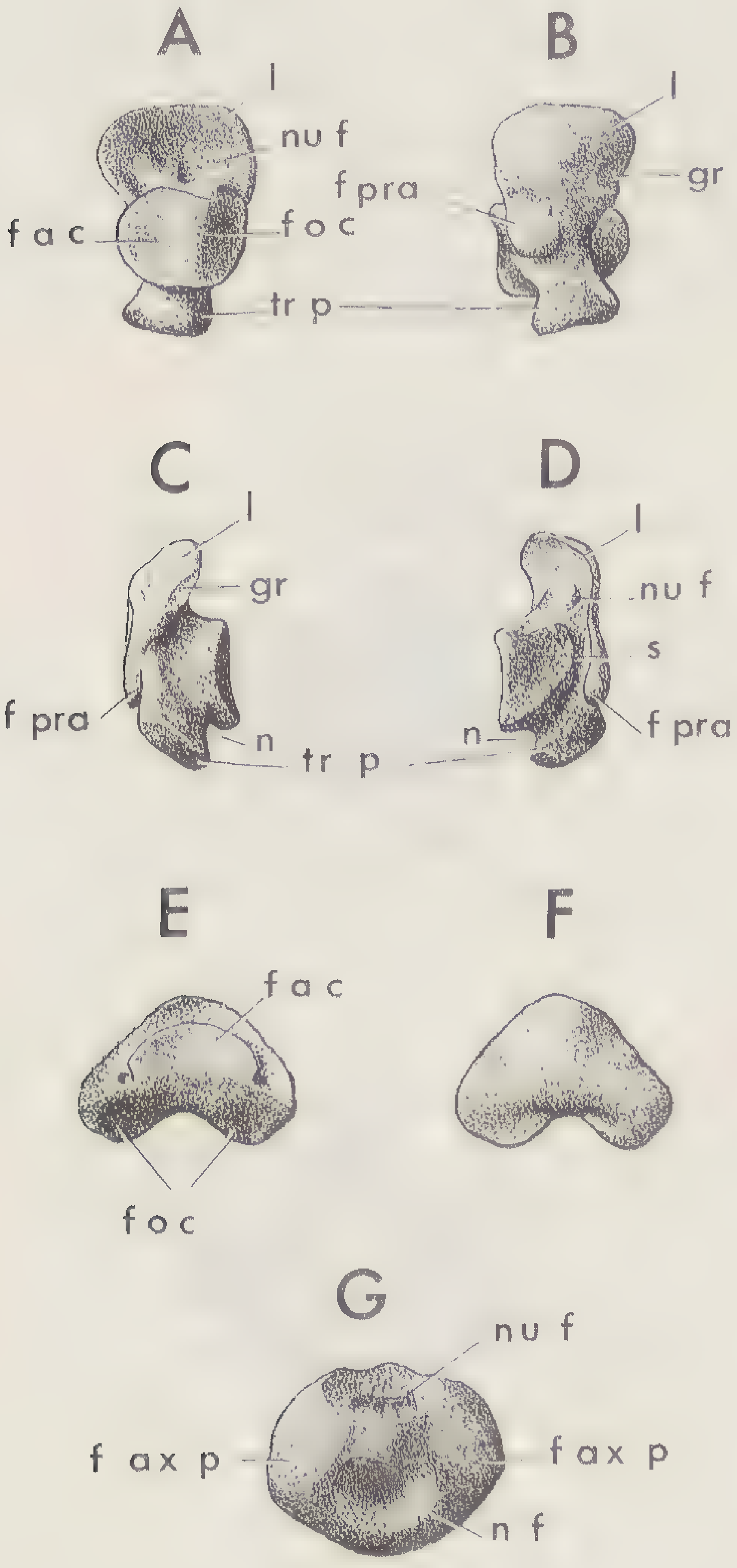

FIG. 1. Components of the atlas in *Thrinaxodon*. A, medial; B, lateral, C, posterior; D, anterior views of the left atlas arch, BMNH R. 511. E, dorsal; F, ventral views of first (or atlas) intercentrum, BMNH R. 511a. G, posterodorsal view of atlas centrum, BMNH R. 511a. Views A–D are arranged to display the total morphology and are not exactly in the anatomical "anterior", "posterior", etc., views. For the anatomically correct position of atlas arch and first intercentrum, see FIGS. 3 and 4. X2. Abbreviations for FIGS. 1–4, 6, 7, 9–11: *a a*, atlas arch; *ap*, anapophysis; *cap*, capitulum; c_1, atlas centrum; c_2, axis centrum; C_1, C_2, etc., first cervical, second cervical etc., *d*, dens; *f a c*, facet for atlas centrum; *f a i*, facet for atlas intercentrum; *f at a*, facet for atlas arch; *f at r*, facet for atlantal rib; *f ax p*, facet for axis pedicle; *f ex*, facet for exoccipital; *f o c*, facet for occipital condyle; *f pra*, facet for proatlas; *gr*, groove, possibly for muscle or ligament attachment; IC_1, atlas intercentrum; IC_2, axis intercentrum; IC_3, intercentrum of C_3; *if*, intervertebral foramen; *l*, lamina; *l r*, ridge on the lamina, possible for muscle or ligament attachment; *n*, notch for first cervical nerve and associated vessels; *n f*, notochordal fossa; *n s*, neural spine; *na*, neural arch; *nu f*, nutrient foramen; *pa*, parapophysis; *pos z*, postzygapophysis; *pra*, proatlas; *pra p*, proatlas process; *pre z*, prezygapophysis; *s*, sulcus for first cervical nerve and vessels; *s a a*, spine of the atlas arch; *tr p*, transverse process; *tub*, tuberculum.

of *Cynognathus* or *Diademodon* (BPI 1675) and in *Gomphognathus* (= *Diademodon*) *kannemeyeri* (Broom, 1903), the atlas centrum is clearly fused to that of the axis. In *Galesaurus planiceps* (UMC R.2721) the fusion is partial, with incomplete closure of the intervening suture. In other specimens of *T. liorhinus* (BMNH R.511a, BMNH R.3731), the atlas centrum has been freed of the axis through acid preparation. In posterior view these centra show a notochordal fossa identical to those developed in the amphicoelous centra of all other vertebrae (*n f*, Fig. 1G). The ventral half of the rim is a broad, rounded lip, as in other centra, which indicates that the

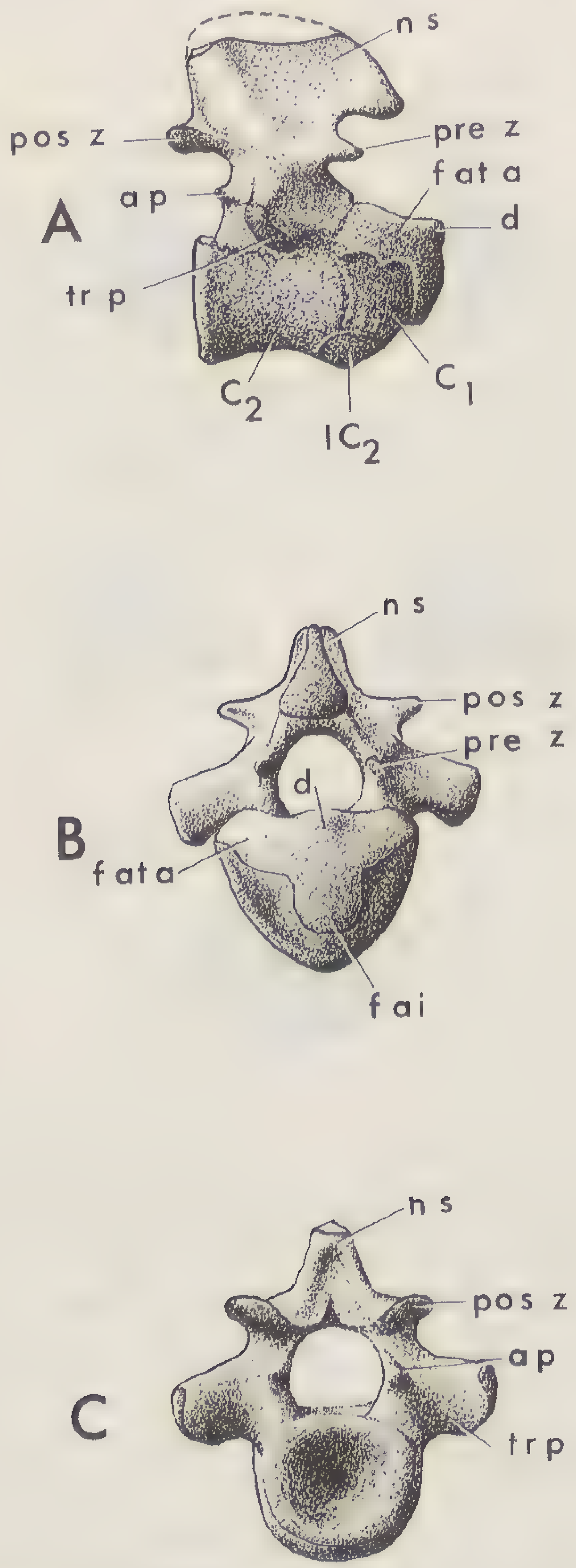

FIG. 2. The axis of *Thrinaxodon liorhinus*, BMNH R. 511. A, lateral; B, anterior, C, posterior. In this specimen the atlas centrum and the second (or axial) intercentrum are attached to the axis. X2. For abbreviations see FIG. 1.

atlas-axis articulation was not ossified and essentially the same as between other vertebrae. However, the dorsal half of the centrum lacks the broad lip which, in other centra, is continuous around the articular rim. In its place are two recessed facets (*f ax p*, Fig. 1G) on the dorsolateral corners, separated medially by a thin, horizontal plate of bone which floors the neural canal. These facets face posterodorsally and very slightly laterally and articulate with facets at the base of the axis pedicles. In *Cynognathus* and *Diademodon* this accessory articulation is obviously not developed because the atlas and axis centra are fused. In galesaurids fusion of axial with atlantal centra was probably a variable feature and perhaps dependent upon the age of the individual.

The atlas neural arch consists of two halves, the laminae of which do not co-ossify to complete the neural arch (*l*, Figs. 1, 4), contrary to the opinion of Broom (1903: 178, 1932b: 263), and of Colbert (1948: 377). There is no neural spine. Medially, each half arch bears facets for articulation with the atlas centrum (*f a c*) and one of the two occipital condyles (*f o c*), and laterally facets for articulation with the proatlas (*f pra*, Fig. 1B, D) and atlantal rib (*f at r*, Fig. 4C). A short but robust "neck" separates the two medial articular facets from the rest of the bone, imparting a greater thickness to this pedicle-lamina area than in post-atlas vertebrae. The medial facets for occipital condyle and atlas centrum are concave and more or less semicircular in outline (Fig. 1A). Their surfaces, intersecting at an angle of about 120°, are divided medianly by a low, slightly concave ridge. In *Galesaurus*, the facet for the occipital condyle is antero-posteriorly longer than the facet for the atlas centrum.

The lateral part of the atlas arch is basically a flat, straplike plate of bone which dorsally forms the lamina of the neural arch (*l*) but ventrally becomes the transverse process (*tr p*, Figs. 1A-D, 4). Above the neural canal, the lamina is nearly horizontal. The medial edge of the lamina is thin and bladelike and usually incomplete. Even in complete specimens (Fig. 3C), however, the edge does not extend medially beyond the occipital and atlas centrum facets. Therefore, the dorsomedial edges of the two halves of the atlas arch could not have met (as is true also for pelycosaurs—cf. Romer and Price, 1940: 108), and the dorsum of the neural canal was probably completed by cartilage or ligament linking the edges. The part of the lamina which projects above the occipital and atlas centrum facets is slightly concave medially and appreciably thickens ventrally. One or sometimes two foramina (*nu f*, Fig. 1A, D) occur at the junction of the plate and the "neck" supporting the articular facets for the condyle and atlas centrum. In *Thrinaxodon* (where there is consistently only a single foramen) there is no obvious exit for this foramen which evidently represents a nutrient supply.

On the dorsolateral surface of the atlas arch lamina is a broad, shallow groove (*gr*, Figs. 1B, C, 3C) which is broadest posteriorly. The lateral edge of the groove, especially in larger cynodonts, is defined by a small tuberosity. The functional significance of these two structures is not clear, especially so because there appear to be no analogous features in pelycosaurs. Possibly they represent a muscle attachment, either an atlanto-axial interarticular or one of the oblique muscles associated with the occipital joint.

In *Thrinaxodon* a rounded sulcus runs between the anterior edge of the lamina and the anterior rim of the occipital facet (*s*, Fig. 1D). The sulcus is covered by the

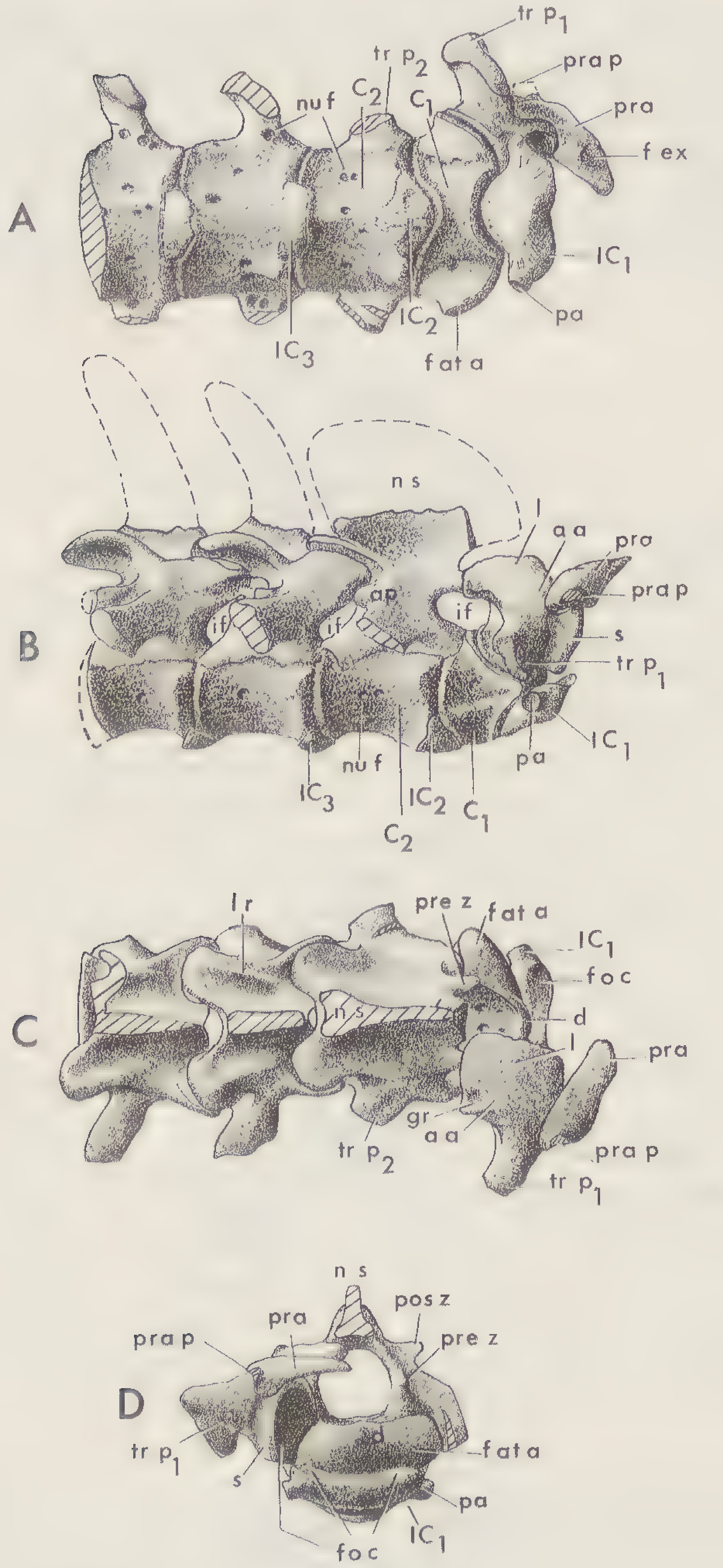

FIG. 3. The first four cervical vertebrae of *Galesaurus planiceps*, UMC 2721. A, ventral; B, lateral; C, dorsal views. D, anterior view of atlas and axis. In this illustration the left atlas arch and proatlas have been removed to reveal details otherwise obscured. X1.6. For abbreviations see FIG. 1. Oblique hatching indicates damaged or missing bone.

proatlas, forming a short canal. Ventrally the sulcus is not covered by the proatlas; it passes posteriorly through a notch (*n*) between the transverse process and the lateral aspect of the facets for the occipital condyle and atlas centrum. The sulcus is lost as a distinct feature on the posteroventral aspect of the transverse process. In *Galesaurus* (UMC R.2721, Fig. 3B), *Cynognathus* and *Diademodon* (BPI 1675, Fig. 4A) the morphology of the sulcus is the same except that the anterior rim of the lamina contacts, and in some cases apparently synostoses with, the anterior margin of the facet for the occipital condyle. The canal is thus formed to the exclusion of the proatlas which nevertheless lies in its normal position across the area of the enclosed canal. The canal and sulcus trace the path of the vertebral artery, vein, and first cervical nerve which, in mammals, generally pass through an atlantal intervertebral foramen and alar notch. The foramen or notch in the mammalian atlas through which the first cervical nerve exits is not, of course, strictly "intervertebral"; however, it is analogous to the true intervertebral foramina and, for lack of a better term, is best designated by that name. In cynodonts, that part of the sulcus covered by the proatlas represents the intervertebral foramen of mammals, while the notch between transverse process and the rim of the medial condyles is equivalent to the alar notch of mammals. Living mammals which normally possess an enclosed first intervertebral foramen sometimes display atavistic tendencies with regard to its enclosure, thereby reverting to a primitive condition. In a specimen of *Didelphis marsupialis* (YPMOC 243), for example, the left foramen is complete but the right is open anteriorly through a failure of ossification, thus creating a deep groove similar to that in *Thrinaxodon*.

A raised, rounded facet for the proatlas is situated between the root of the transverse process and the base of lamina (*f pra*, Fig. 1B-D). The facet is slightly convex. In *Thrinaxodon* it overhangs anteriorly the sulcus for the vertebral artery and vein and first cervical nerve. In other cynodonts it often completely covers the sulcus by contacting the anterior rim of the atlantal occipital facet.

The atlantal transverse process projects posterolaterally and somewhat ventrally and its flat anterior and posterior surfaces are oriented almost vertically (*tr p*, Figs. 3C, D, 4). In most specimens the process is deeper dorsoventrally at its distal (free) end than at its base. The narrowing of the transverse process is due to the presence, across the ventral margin of its proximal end, of a notch for passage of the first cervical nerve and associated vessels (*n*, Figs. 1C, D, 4A, C). The process is otherwise rectangular, with a long, narrow facet for the atlantal rib at its distal end. The facet, which is either slightly convex or flat, faces posterolaterally and slightly ventrally. In *Cynognathus* and *Diademodon* the notch at the root of the transverse process is relatively small and does not significantly alter the outline of the process; in other respects the transverse process is like that of *Thrinaxodon* or *Galesaurus*.

In no cynodont is a transverse foramen known. In mammals, the transverse foramen pierces the posteromedial aspect of the expanded atlas transverse process for passage of the vertebral vein and artery. In some mammals, e.g., the Egyptian mongoose (*Herpestes ichneumon*), the transverse foramen pierces the dorsal surface of the atlas wing anteriorly in a fossa shared with the exit of the intervertebral foramen. The transverse foramen then traverses the length of the wing as a canal and exits at the

posterior edge of the wing adjacent to the atlanto-axial joint. This and other variations of its course do not alter the basic fact that it represents enclosure of vessels by reorientation of the bone in response to new muscular requirements. The foramen obviously arose during mammalian evolution in conjunction with the expansion of the transverse process into a broad, flat wing for increased muscular attachment. Commonly the wing of the atlas extends posteriorly almost to the atlanto-axial intervertebral foramen and, during its evolutionary development, has evidently encircled the blood vessels. The shallow notch across the ventromedial aspect of the cynodont atlantal transverse process possibly represents the initial stage of formation of a transverse foramen and could have been bridged by fibrous tissue or even cartilage. In primitive mammals which do not possess a transverse foramen, e.g., *Ornithorhynchus*, *Didelphis*, there is a deep notch in the posterior border of the atlas wing which represents the incomplete development of the foramen.

The atlas intercentrum is known from *Thrinaxodon* (BMNH R.511a, Fig. 1E, F), from *Galesaurus* (UMC R.2721, IC_1, Fig. 3) and from *Cynognathus* and *Diademodon* (BPI 1675, IC_1, Fig. 4). The intercentrum is a moderately thick, wedge-shaped bone. Viewed from above or below, its outline is variable; in *Cynognathus* and *Diademodon* it is oval and somewhat irregular, in *Thrinaxodon* it is triangular, and in *Galesaurus* it is narrowly rectangular except for a protruding lip which articulates with the atlas centrum. The ventral surfaces of all intercentra are broadly convex. On its dorsal surface the first intercentrum bears a facet for the atlas centrum posteriorly (*f a c*) and two facets for the occipital condyles anteriorly (*f o c*, Figs. 1E, 4). The atlas centrum facet is oval in outline and is shallowly concave, especially along its transversely oriented long axis. This facet is confluent with part of the posterior border of the occipital facets which face anterodorsally and slightly medially. In *Thrinaxodon, Cynognathus* and *Diademodon*, a rounded notch in the middle of the anterior margin of the intercentrum partially separates the two occipital facets; this notch is not as deeply incised in *Galesaurus*. Each of the posterolateral corners of the intercentrum bears a posterolaterally directed parapophysis (*pa*, Fig. 4). On the apex of the parapophysis is a round or oval facet for the capitulum of the atlantal rib. A broad, flat lip, sometimes in the form of a distinct tubercle, projects posteriorly from beneath the atlas centrum facet and probably functioned in ligamentous attachment to the atlas centrum. On well-preserved first intercentra, a (?nutrient) foramen pierces the dorsal surface on either side of the facet for the atlas centrum (*nu f*, Fig. 4B). There are also foramina, variable in number, on the ventral surface, but it is unlikely that any of these communicate with those on the dorsal surface.

Proatlas

MORPHOLOGY. All cynodonts for which the atlas arch is known have a proatlas facet, but an intact proatlas ossicle is a rarity. A proatlas ossicle is preserved in articulation with the atlas arch and occiput in a Munich Museum specimen of *Gomphog-*

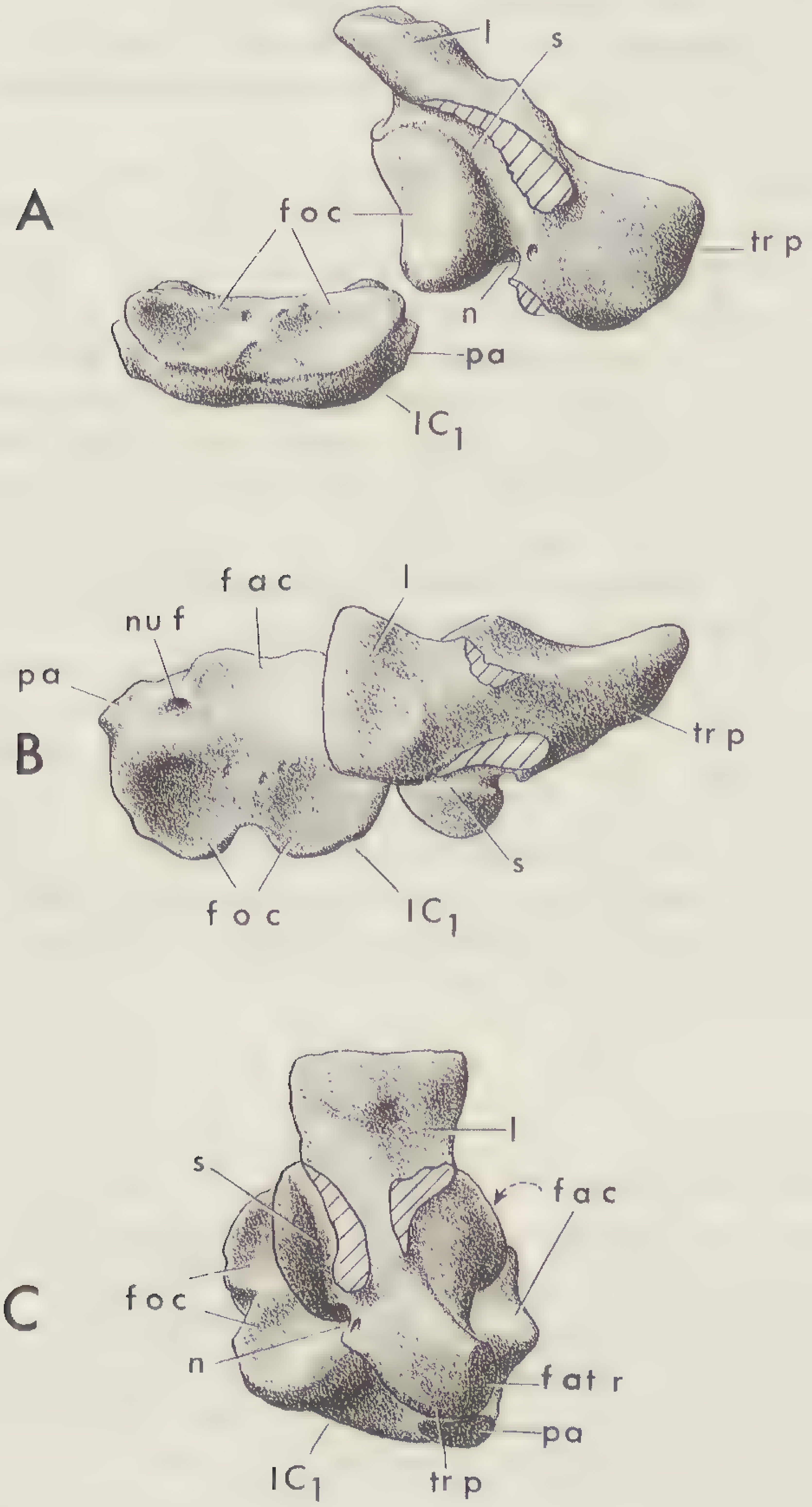

FIG. 4. The first intercentrum and left atlas arch of cf. *Cynognathus* (?*Diademodon*), BPI 1675. A, anterior; B, dorsal; C, lateral views. The two elements are probably not from the same individual. They are arranged in the approximately correct anatomical relationship. X1. For abbreviations see FIG. 1. Oblique hatching indicates damaged or missing bone.

nathus (= *Diademodon*), the lower jaw of which was described by Janensch (1952: 237). Proatlas ossicles are described by Broom (1903) in *Gomphognathus* (= *Diademodon*) *kannemeyeri* and in *Trirachodon kannemeyeri*. A proatlas is known in one specimen of *Thrinaxodon* (USNM 22812). Proatlas ossicles are also preserved in a

specimen of *Procynosuchus* in the Rubidge Collection (A. W. Crompton, personal communication) but I have not examined this specimen. Parrington (1934) described and figured the proatlas ossicles of *Galesaurus planiceps* (UMC R.2721). Parrington's description requires modification in light of the additional preparation undertaken on this well-preserved specimen.

In outline the proatlas ossicles of *Galesaurus* are trapezoidal (*pra*, Fig. 3B, C), not rhomboidal as originally described and figured. The slightly concave ventral margin is more or less horizontal and is the thickest part of the plate. On the lateral surface, halfway along the ventral margin, is a process that has been broken off on both sides (*pra p*, Fig. 3A-D). Parrington incorrectly figures this tuberosity at the junction of the ventral and anterior margins of the plate. The process is well preserved in the specimen of *Diademodon* described by Janensch (1952) and is well known in the South American traversodontid *Exaeretodon* (Bonaparte, 1963a). In the former the process is rectangular in cross-section, dorsoventrally compressed and wider anteroposteriorly. In length it slightly exceeds that of the atlas transverse process and therefore extends laterally beyond the tip of the atlas transverse process.

The anterior and posterior margins of the proatlas ossicle of *Galesaurus* are approximately parallel and incline cranially at an angle of about 20° from the vertical. The convex anterodorsal margin is the thinnest part of the plate. The plate as a whole is bowed and slightly twisted so that the ventral (or lateral) half faces dorsolaterally while the dorsal (or medial) half faces posterodorsally. The internal surface of the plate bears two facets, one at its posteroventral corner for articulation with the atlas, the other near the junction of its anterior and anterodorsal margins for articulation with the exoccipital (*f ex*, Fig. 3A).

Axis

MORPHOLOGY. The second or axial intercentrum has been recovered only with articulated specimens and thus the morphology of its articular surfaces is not completely known. It is best preserved in *Galesaurus planiceps* (UMC R.2721, IC_2, Fig. 3A, B). Like other intercentra, it probably has the general structure of a curved plate. The ventral surface, diamond-shaped in outline (Fig. 3A), is convex transversely as well as anteroposteriorly. The anterior edge is markedly convex and the posterior rim of the atlas centrum is reflected anteriorly to receive it. The posterior edge is nearly straight except for a slight backwardly projecting tubercle.

The axis centrum of cynodonts is similar to the centra of other postaxial cervical vertebrae (C_2, Figs. 2, 3). Presumably the centrum was amphicoelous, although fusion or attachment by matrix to the atlas centrum prohibits examination of the anterior face of any known axis centrum. The lateral sides of the centrum are concave anteroposteriorly, meeting along the midventral line to form a keel. The sides are perforated by a number of nutrient foramina (*nu f*) in variable patterns. The dorsum of the centrum is beveled by three surfaces, two of which are dorsolateral and join with the pedicles, the third lying between the two and forming a broad groove for the floor of the neural canal. In the center of the canal floor is a fossa of unknown function which is similarly developed in all other postaxial centra. Broili and Schröder

(1936: 64–65) observed the same feature in cynognathid cervical vertebrae. They discussed the possibilities that it was related to the "marrow cavity" (actually, cancellous bone) of the centrum or that it formed as a result of an unusual pattern of synostosis of the neural arch to the centrum. At present, neither of these possibilities can be given a definitive evaluation.

The pedicles of the axial arch join the centrum along its entire length except posteriorly where the rim of the centrum is continuous about the entire articular face. The anterior quarter of each pedicle overhangs the anterior articular face of the axial centrum and articulates, at an angle of about 45° from the horizontal, with the posterolateral corners of the atlas centrum. The articulations between the pedicles and both centra appear to be synchondroses. The articulation between atlas and axis centra, and the contact between axial pedicles and atlas centrum, are apparently partially synostosed in one specimen of *Thrinaxodon liorhinus* (BMNH R.511).

The transverse processes of the axis are robust and rectangular. They project laterally and somewhat posteroventrally, each bearing on its slightly swollen terminus an oval facet for the tuberculum. The orientation of the transverse processes are more horizontal than are those of post–C2 vertebrae (Fig. 3B).

The prezygapophyses, diminutive in size compared to the postzygapophyses, are not preserved in most specimens. In *Thrinaxodon liorhinus* (BMNH R.511) and *Galesaurus planiceps* (UMC R.2721), the processes are thin blades which attenuate to a blunt point (*pre z*, Figs. 2A, 3C). Their orientation conforms to that of the laminae from which they arise, i.e., the external surface facing dorsolaterally, the internal facing ventromedially. In neither *T. liorhinus* nor *G. planiceps* can distinct articular facets be detected on these processes. The postzygapophyses are robust and bear facets which incline ventrolaterally at an angle of about 45° (*pos z*, Fig. 2). Beneath each postzygapophysis is an anapophysis (*ap*, Figs. 2A, C, 3B) which projects posteriorly from the pedicles at the level of the top of the transverse process. In recent mammals, anapophyses usually represent the point of insertion of a part of the longissimus muscle system.

The spinous process or neural spine is a broad, hatchet-shaped blade (*n s*, Figs. 2, 3). In cross-section it is very thin through the middle, but both anteriorly and posteriorly it is much increased in thickness and is terminated, at the anterior end at least, by a tuberosity. In *Thrinaxodon* and *Galesaurus*—the only two genera for which nearly complete spines are known—there are two fossae for muscular origin on each side of the blade. One is just above the base of the prezygapophysis; the other lies more or less in the center of the blade surface. In all known specimens the thin dorsal edge of the blade is at least partly lost. Brink (1954: 117) described the dorsal edge in *Thrinaxodon liorhinus* (NMB C.392)[2] as concave. However the specimen to which he referred is broken in this area. The type of *Thrinaxodon liorhinus* (BMNH R.511) is less damaged and shows that the edge was at least straight and probably convex.

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[2] Erroneously listed by Brink (1954) as C.292, although his caption to text-figure 1 correctly labels it C.392.

Atlantal and Axial Ribs

MORPHOLOGY. It is certain that both the atlas and the axis of cynodonts bear ribs because the shape of their transverse processes is no different from those of other rib-bearing cervical vertebrae. Parrington (1934: 48) described a rib associated with *Galesaurus planiceps* (UMC R.2721) which he believed to be an atlantal rib. Further preparation (in acid) on this specimen has been undertaken since Parrington's original description, and, as this remains the only known rib associated with the first two cervical vertebrae, further description is warranted.

Originally the complete rib was 9 mm long and 4 mm wide at its midpoint, expanding distally to a spatulate terminus. The proximal end was lodged between the atlas transverse process and the atlas centrum and was thus obscured. With further preparation the distal end was lost but the proximal end was freed. The proximal end is a very thin, spatulate plate averaging 0.8 mm in thickness. There is no rodlike thickening anywhere on the plate to denote a central axis or shaft. The tuberculum is a rectangular process which projects only a short distance from the plate. The tubercular facet is 3 mm long, not 3.5 as reported by Parrington, is approximately 1 mm wide at its dorsal end, and is constricted in the middle which imparts a figure 8 outline. The facet of the atlas transverse process has a similar outline, but is almost 5 mm long and, at the dorsal end, 2 mm wide. This disparity in size is difficult to account for unless there was a considerable amount of cartilage or connective tissue intervening. The capitulum is a small tubercle located on the ventral margin of the plate, 2 mm from the base of the tuberculum. Its diameter is about half that of the parapophysis on the atlantal intercentrum. This disparity in size is similar to the anomalous tuberculum-diapophysis relationship and must have required an unusual amount of connective tissue or cartilage to complete the articulation. The rib has been somewhat crushed, but it appears probable that its platelike surface was slightly concave medially and convex laterally.

2. THE EVOLUTION OF THE MAMMALIAN ATLAS-AXIS COMPLEX

Specializations of the cynodont atlas and axis represent an initial stage in the evolution of a mammalian atlas and axis. In order to evaluate these specializations, reference must be made to the atlas-axis structure and function in pelycosaurs as well as in mammals. For clarity, separate consideration is given to each of the major functional aspects of the atlas-axis joint.

The Position of the Occipital Condyles

The most obvious difference between reptiles and mammals at the atlanto-occipital joint lies in the condyles—reptiles being monocondylic and mammals bicondylic. Equally obvious is the fact that the mammalian condition is derived from the reptilian

by a "splitting" of the originally single condyle. The position of the mammalian condyles is not so easily explained, for they invariably occur lateral to the foramen magnum. If the course of condylar evolution had been a process of simple bisection, the expected position of the two mammalian condyles would be ventrolateral to the foramen magnum. But mammalian condyles have apparently migrated dorsally as well as laterally. In cynodonts, the position of the condyles with respect to the foramen magnum is not quite mammalian and in fact is intermediate between an early synapsid (pelycosaur) stage and that of a typical mammal. The shift in the position of the condyles with respect to the foramen magnum is almost certainly related to other mammalian specializations of the atlanto-occipital joint. The most important of these specializations involves an increased ability to flex and extend the head.[3] Therefore, the position of mammalian condyles is also possibly related to an increase in the range of flexion and extension—as the following functional analysis attempts to demonstrate.

The single occipital condyle of pelycosaurs is convex, with a subcircular, often nearly triangular, outline (Fig. $5A_2$). It is composed of equal contributions from the paired exoccipitals and a median basioccipital and lies directly beneath the foramen magnum. When the head flexes or extends, the axis of cranial movement is a theoretical line drawn transversely through the condyle. The spinal medulla, lying entirely above the axis of movement, must be compressed during extension and stretched during flexion. For x degrees of flexion, for example, the amount of spinal medulla elongation is given by

$$2 \pi r \left(\frac{x}{360} \right)$$

where r is the distance between the axis of rotation and a selected point in the spinal cord. This assumes that stretching occurs along an arc. If the elongation is linear, then the amount is given by

$$\cos \frac{x}{2} = \frac{\frac{x}{2}}{r}$$

and is slightly less. Spinal cord deformation at the reptilian atlanto-occipital joint is the result of a large r value, which is constant for any selected point, and a variable x (degrees of flexion) value.

There is no comparative data on the elastic limits of tetrapod spinal medullae. However, in terms of specializing for maximum extension and flexion, an obvious mechanical advantage results from a reduction of the value of r so that the amount of spinal medulla deformation per degree of flexion or extension (x) is minimized. Such a reduction is possible if the spinal medulla intersects the axis of flexion and extension by "passing through" the occipital condyle. In this case the r values vary from zero (at the intersection of the rotational axis and the spinal medulla) to an amount equal to the radius of the spinal cord itself. Thus, for a given diameter of spinal medulla, values of x produce the least deformation possible. Mammals have evolved precisely this

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[3] Flexion and extension are here employed with respect to the head and neck as in human anatomy. Flexion is movement downward and forward, extension is movement upward and backward.

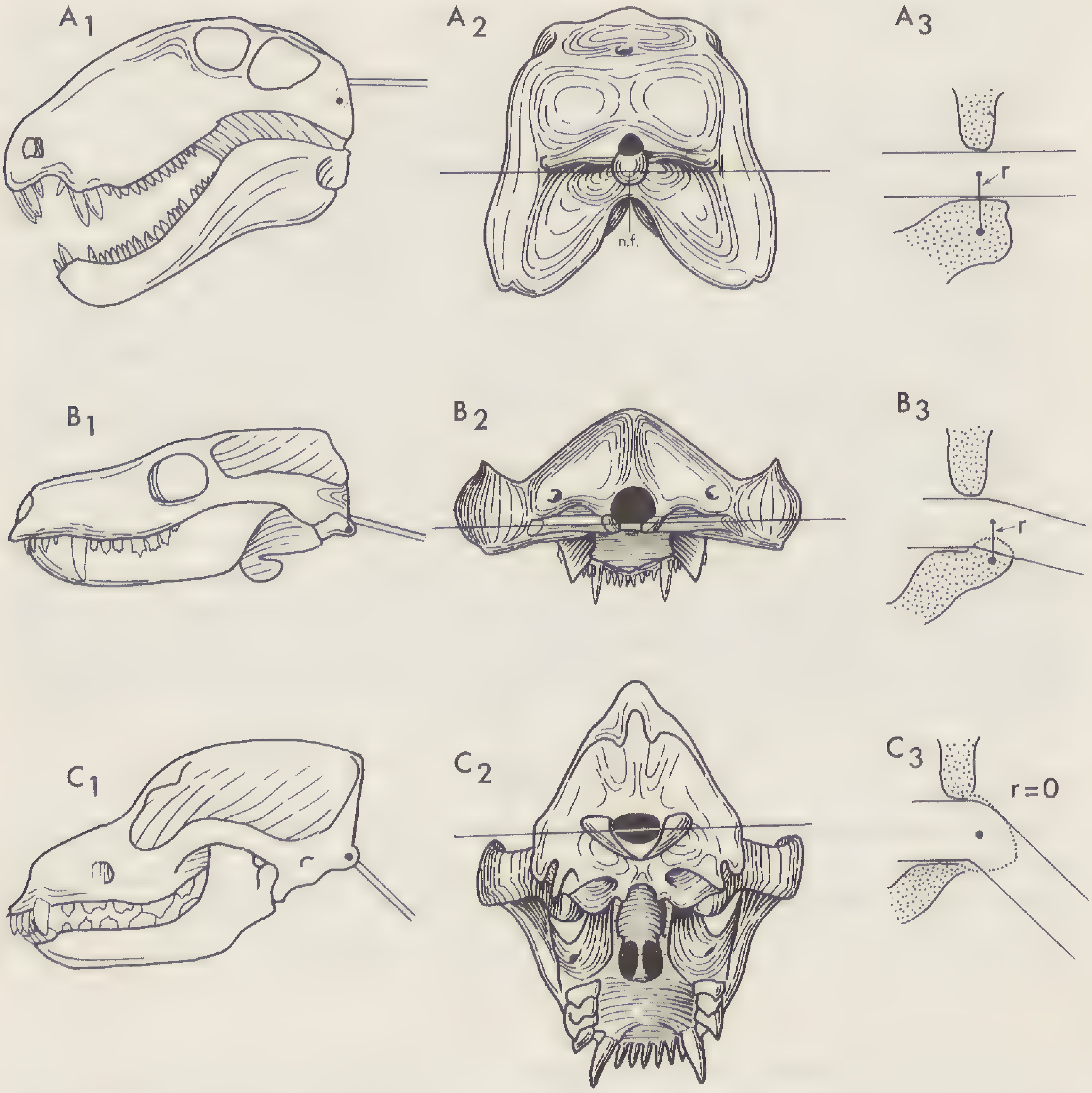

FIG. 5. Diagrammatic representation of A, *Dimetrodon*; B, *Thrinaxodon*; and C, *Canis*, representing stages in the evolution of mammalian occipital condyles. Subscript 1, lateral view of skulls with double line indicating position of spinal medulla relative to transverse axis of flexion-extension, represented by black dot. Subscript 2, occipital view of skulls, i.e., looking along spinal medulla into foramen magnum, with single line representing the transverse axis of flexion-extension. Subscript 3, sagittal sections through the foramen magnum. r = vertical distance between axis of flexion-extension and the center of the spinal medulla. Not to scale.

arrangement (Fig. 5C_3). The position of the condyles lateral to the foramen magnum entails the passage of the axis of flexion and extension through or close to the spinal medulla center. This relationship, one of the most invariable of mammalian anatomy, accounts for the lateral position of the condyles relative to the foramen magnum.

The occipital condyles of most cynodonts are clearly separate[4], but they do not occupy a typically mammalian position. Instead, cynodont condyles occur at the ven-

trolateral "corners" of the foramen magnum (Fig. $5B_2$; see Brink and Kitching, 1953b, for *Cistecynodon*; Broili and Schröder, 1934, for *Cynognathus*; Brink, 1954, for *Glochinodontoides*). In this position, the axis of flexion and extension is nevertheless relatively closer to the spinal medulla than it is in pelycosaurs and is intermediate between the basic reptilian and mammalian patterns.

These conclusions are similar to those reached by Hayek (1927: 334–336), but were independently derived. Hayek noted that in living amniotes the axis of flexion and extension—his "frontal Bewegungsachse"—is variable in position with respect to the foramen magnum. He was able to show, using both osteological models and cadavers, that in birds (essentially as in Fig. 5A) there is considerable displacement of a point marked on the spinal medulla during flexion and extension. Employing the same technique in the study of cervico-occipital flexion and extension in man (as in Fig. 5C), he found essentially no displacement. While Hayek's data are consistent with the analysis given here, neither demonstrate the basis for the necessity of limiting spinal medulla or medulla oblongata deformation in mammals. Either the elastic properties of the spinal medulla are approximately the same in the two classes, in which case other factors require the elimination of deformation at this joint in mammals, or the elastic properties are not the same, in which case the mammalian arrangement of condyles is an adaptation for maximum movement and minimum deformation. At present there are no data on which to base a choice between these alternatives.

Cervico-Cranial Flexure and the Position of the Atlanto-Occipital Joint

The evolution of a bicondylic occipital joint in mammals is accompanied by certain postural changes of the head and neck. In most mammals, the axis of the cervical vertebral series ascends toward the skull (Fig. $5C_1$). The longitudinal axis of the skull, however, is normally inclined in an opposite direction, so that the rostral end of the skull is lower than the occipital end (see de Beer, 1947). Hence there is an angulation between the cranial and cervical axes. This feature is also accompanied by a relative displacement of the foramen magnum and occipital condyles to the extreme posteroventral aspect of the skull (Fig. $5C_2$). In most Paleozoic as well as in many recent reptiles, the cervical axis is nearly horizontal and more or less continuous with the longitudinal cranial axis; in normal posture the head is little or not at all elevated above the level of the axial skeleton (Fig. $5A_1$). The atlanto-occipital articulation is located at or near the midpoint of the occipital surface so that there is about as much cranial mass above the occipital condyle as below it (Fig. $5A_2$). These basic relationships, which in reptiles actually are not much advanced beyond a piscine stage, not only limit flexion and extension, but provide a relatively short moment arm for extensor musculature with which head posture is maintained. The anatomy of the mammalian

[4] Procynosuchids have a kidney-shaped condyle which is only incipiently bicondylic; see Brink (1963: 60).

atlanto-occipital articulation is partly explicable in terms of permitting greater freedom in extension and flexion and providing a longer lever arm for extensor musculature.

In generalized mammals where the normal curvature of the spine in the anterior thoracic and posterior cervical regions results in an ascending axis toward the skull and the longitudinal axis of the skull is characteristically oriented in the opposite manner, the spinal medulla does not exit from the foramen magnum in a strictly caudal direction. Instead, it passes posteroventrally to conform with the descending neural canal. The condyles and foramen magnum are located more or less at the juncture of the occipital and basioccipital surfaces. This arrangement, associated with the angulation of the cranial and cervical axes, provides a relatively greater amount of space for flexion and extension than does the reptilian arrangement (compare Fig. $5A_1$ and $5C_1$). Cynodonts appear to be more mammalian than reptilian with regard to the location of the occipital condyles, and in *Thrinaxodon* at least, the foramen magnum is directed posteroventrally, which indicates angulation of the cranial and cervical axes (Fig. $5B_1$). It is difficult to be positive about the posture of the neck in cynodonts. The relatively high neural spines of the cervical series are consistent with an interpretation of well-developed extensor musculature, but do not necessarily establish an ascending cervical axis. From evidence of the angulation of cranial and cervical axes, it appears likely that the cynodont head and neck were at least somewhat elevated, thus approximating a mammalian condition. The parasagittally oriented zygapophyses of the anterior thoracic vertebrae would certainly permit such a posture.

The Origin and Homology of the Dens

Cynodonts do not possess a typical dens, or odontoid process, which in mammals forms a toothlike or tonguelike projection of the axis into the atlas ring. Nevertheless, the cynodont atlas-axis complex is important to an understanding of the structural evolution of the dens and, together with certain osteological and developmental evidence from mammals, clarifies its homology. Standard reference works of mammalian anatomy state that the dens is shown developmentally to represent the atlas centrum (e.g., Sisson and Grossman, 1953: 32; Young, 1957: 150; Crouch, 1965: 145; etc.). In fact, the development of the dens is more complex than has been generally acknowledged and it is necessary to review the embryological evidence in some detail before considering its evolutionary history.

Goodrich (1930: 69–70) summarized the evidence supporting the conclusion that in certain reptiles, birds and mammals, the dens (or, in reptiles, the atlas centrum) forms from two chondrification centers. Goodrich concluded, following other authors, that the anterior chondrification center represents an anterior sclerotomite; the posterior sclerotomite of the same sclerotome enters into the formation of the atlas. Thus the proatlas is the neural arch (dorsal half) ossification of this anterior sclerotomite, and the anterior chondrification center of the dens is the pleurocentral (ventral half) manifestation of the same anterior sclerotomite. The contribution of a "pro-atlantal" sclerotomite to the tip of the dens has subsequently been confirmed in *Mus* (Dawes, 1930), in *Peromyscus* (Sensenig, 1943) and in man (Sensenig, 1957). Hayek's (1924)

observation that in reptiles the ventral half of a "pro-atlantal" sclerotomite contributes to the anterior half of the atlas centrum establishes that this developmental process is basically the same as in mammals. Therefore, there was no radical modification in development during the reptilian-mammalian transition. The remainder of the dens, i.e., its posterior chondrification center, is universally acknowledged to be derived from sclerotomic material homologous in position to the sclerotomic material which gives rise, in reptiles, to the atlas centrum. On this basis the developmental equivalence of the mammalian dens with the reptilian atlas centrum is established.

The supposedly well-established developmental history of the dens still does not account for the evolution of its characteristic shape and relations. For example, if the dens is a structurally altered atlas centrum, then what selective processes account for its diminution and encapsulation into the atlanto-axial joint? Furthermore, the developmental evidence has never been used to define the exact contact between the axis centrum and dens ("atlas centrum"). Apparently neither of these aspects is well understood. Romer (1962: 172) stated that the dens also includes the intercentrum of the axis, while Lessertisseur and Saban (1967: 601) admitted the additional possibility that the axial intercentrum may be completely lost. Miller et al. (1964: 52) claimed that in the dog the dens "is morphologically the caudal part of the body of the atlas. . .", implying thereby that a cranial part has not been accounted for or is lost. Authors seldom define a line of separation between dens ("atlas centrum") and axis centrum. Since, however, the dens is invariably equated with the whole of the atlas centrum (plus a proatlas rudiment), the obvious conclusion would be that the division of dens from axis centrum occurs at the base of the dens.

The homology and structural evolution of the dens is clarified by reviewing the basic features of the pelycosaur, cynodont and monotreme atlas-axis complexes. In pelycosaurs and cynodonts, the atlas centrum is clearly a separate ossification and alone bears the facets which articulate with the two halves of the atlas arch. The atlas centrum of these forms is primitive insofar as its dimensions approximate those of other cervical centra, the only exception being that in length it is somewhat shorter than other centra.

In pelycosaurs a notochordal remnant was present in the atlanto-occipital joint, for both the occipital condyle and anterior face of the atlas centrum bear a slight notochordal fossa just above center (Romer and Price, 1940: 64; *n f*, Figs. $5A_2$, 6C, D). This notochordal remnant might have been in the form of a nucleus pulposus, such as typically occurs in mammals between all vertebrae except in the sacral, atlanto-occipital and atlanto-axial joints. If this were the case, a true synovial joint was not present, but rather an amphiarthrodial joint in which a fibrocartilaginous disc (perforated through the center for the nucleus pulposus) connected occiput to atlas centrum. This type of joint would have greatly restricted the range of movement. However, it appears more likely that at least some form of synovial capsule in this region was part of the heritage of early synapsid reptiles. Romer and Price (1940: 108) concluded that in pelycosaurs most movements of the head with the atlas-axis joint occurred at the altanto-occipital joint. In order for this simple ball-and-socket joint to have permitted even limited degrees of flexion, extension, abduction and rotation, a synovial joint of some sort must have been present. Furthermore, a synovial joint would be required by the apparently close apposition of the anterior surface of the atlas cen-

trum, arches and intercentrum with the occipital condyle (except, of course, the small notochordal pit on each side). In typical post-C2 vertebrae, however, the centra are deeply amphicoelous and notochordal. The adjacent rims of these centra lack the finished surface typical of bone covered with articular cartilage and were probably bound together by ligaments (Romer and Price, 1940: 96) as in the annular ligaments of mammals. Smoothly textured bone is evidence of articular cartilage and hence a synovial cavity. The occipital condyle and anterior surface of the atlas centrum possess just such surfaces, and therefore it is reasonable to conclude that some sort of a synovial capsule, with its typical membranes and fluid, was already developed in pelycosaurs. If the atlanto-occipital joint in pelycosaurs were of a synovial type, then the notochordal pits still remain to be explained. Possibly they functioned in attachment of an atlanto-occipital ligament within the synovial capsule. Ligaments within an articular capsule, e.g., the cruciate ligaments of the knee, are known to be an important mechanism for maintaining joint integrity and control.

Whether the notochordal pits of pelycosaurs represent a gelatinous or ligamentous remnant, there is no question that the pits are absent in cynodonts and that their associated structure must have been altered or displaced. With the doubling of condyles, the notochordal pit of the originally single condyle is of course lost. The area on the anterior face of the cynodont atlas centrum corresponding to the position of the pelycosaurian notochordal pit is smooth, with no sign of an indentation (Fig. 2B). The only possible structural manifestation of a notochordal rudiment is in a slightly more dorsal position, at a level just below the floor of the neural canal. In *Thrinaxodon* (BMNH R.511, BMNH R.511a) and *Galesaurus* (UMC R.2721), a slight protuberance occurs at the point, here interpreted as an incipient dens (*d*, Figs. 2A, B; 3C, D). As a median structure separating the two lateral facets for the neural arch halves, it lies in a position analogous to that of the mammalian dens. A similar feature is present on two other axes (DMSW R.204, DMSW R.205) of large, unidentified cynodonts, probably, but not certainly, *Diademodon*, and also on a separate atlas centrum from either *Cynognathus* or *Diamemodon* (BPI 1675). An incipient dens has also been identified in the South American traversodontid *Massetognathus pascuali* (Jenkins, 1970a). This proturberance is not found in all known cynodont axes but it is so subtle a feature that it easily might be lost through plastic deformation of the fossil or through careless preparation. After examining a cast of Broili and Schröder's (1934) ?*Gomphognathus* axis, which does not show this feature, I have concluded that this specimen has undergone deformation. The type of *Cynognathus crateronotus* (BMNH R.2571), which also lacks this feature, has been somewhat crudely prepared.

The generally held belief that the mammalian dens represents the atlas centrum has led several authors (e.g., Seeley, 1895b) to refer to the entire atlas centrum in therapsids as a dens. Lessertisseur and Sigogneau (1965) claimed that dinocephalians, dicynodonts and cynodonts all possess an "apophyse odontoide". Were these authors referring to the atlas centrum or some peg-like process of the axis? The atlantal centra of the dinocephalians and dicynodonts that I have examined are generally similar to those in pelycosaurs and do not warrant the term odontoid process; there is no trace of a dens in these forms. Hoffstetter and Gasc (1969) used the terms odontoid process and atlas centrum interchangeably in reference to the atlas centrum of living reptiles. This nomenclatural synonomy should be avoided if the odontoid process (or dens)

and atlas centrum of mammals are not exactly equivalent structures (as will be demonstrated more fully below). The distinction is all the more important in view of the possibility that some reptiles have independently evolved a dens and ligaments analogous to those in mammals (see p. 41).

Developmentally the mammalian dens is intimately associated with a notochordal remnant which becomes the apical ligament (cf. Goodrich, 1930: fig. 61; Gadow, 1933: 95, 311; Gray, 1959: 355). The apical ligament connects the apex of the dens with the basioccipital. The evolutionary history of the notochordal remnant between occiput and atlas is therefore quite different from that between other vertebrae, where it forms the nucleus pulposus (see Williams, 1908). Not only are there obviously different structural specializations represented, but also the relative positions of the two are not the same. The nucleus pulposus retains its primitive position along an axis which pierces the centers of the centra. The notochordal segment that is represented by the apical ligament has apparently migrated dorsally so that it no longer occupies a precisely intercentral position. This migration was already underway in pelycosaurs, for the notochordal fossa is slightly above center on the anterior face of the atlas (*n f*, Fig. 6C, D). In cynodonts further migration carried the notochordal remnant still more dorsally to a level just below the floor of the neural canal, approximating the mammalian condition. During the pelycosaur-cynodont transition, the structure (as well as the function) of the notochordal remnant was altered. In pelycosaurs the notochordal remnant probably retained some of the characteristics of a primitive notochord, being enclosed in a reduced but nevertheless primitive amphicoelous

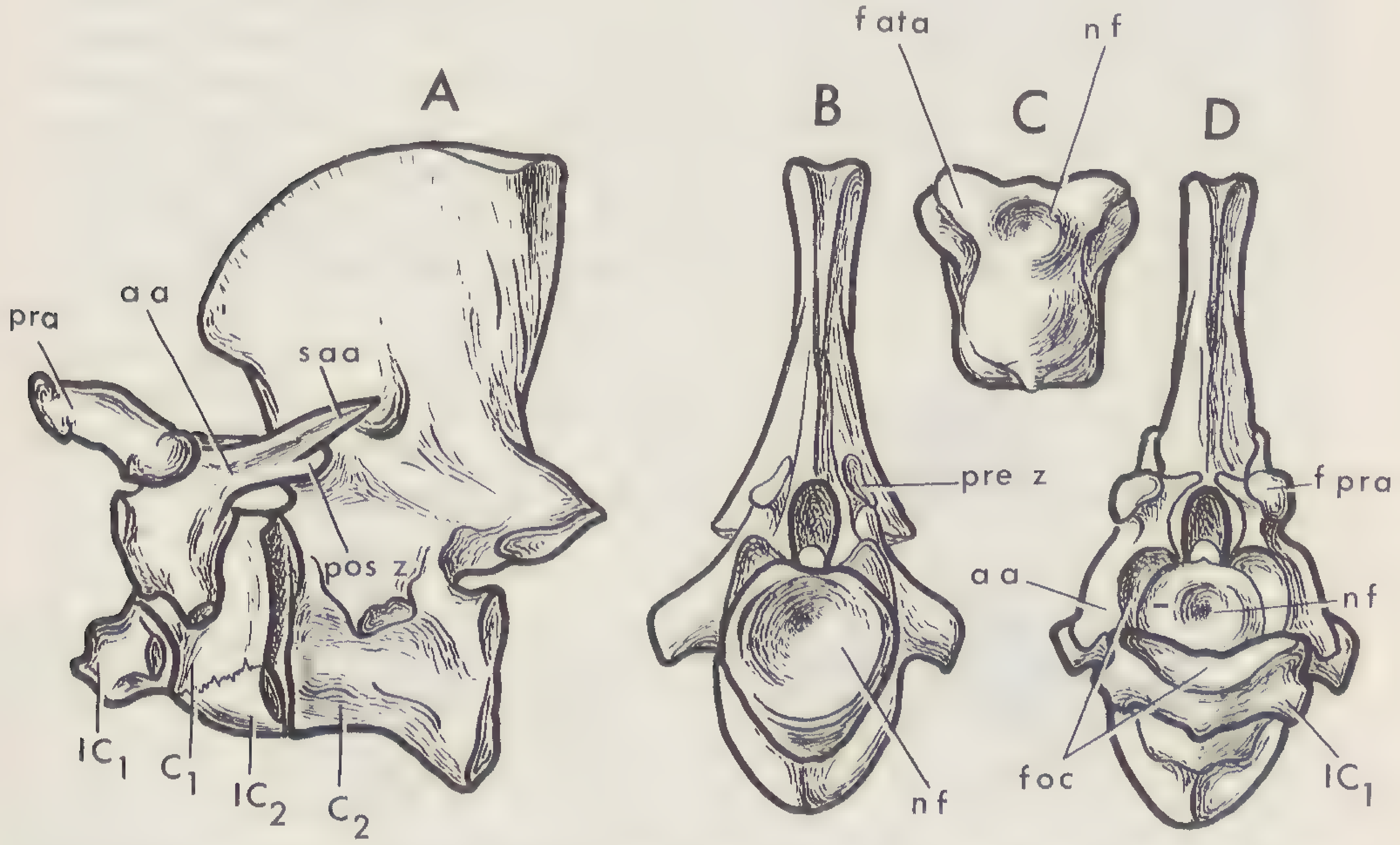

FIG. 6. The atlas and axis of the pelycosaur *Ophiacodon retroversus*, after Romer and Price, 1940: fig. 44. A, lateral view of complete atlas-axis complex. B, anterior view of axis. C, anterior view of atlas centrum. D, anterior view of atlas-axis complex, proatlas ossicles removed. X0.7. For abbreviations see FIG. 1.

concavity. In cynodonts a basic alteration of the structure of the notochordal remnant would account for the loss of the notochordal fossa and the development of an incipient dens. An "apical ligament" probably extended to the basioccipital between the condyles, thus strengthening the atlanto-occipital articulation. At a later and as yet unknown stage the caudal part of the ligament may have been strengthened by ossification in situ or, with the same result, replacement by an increasingly longer protuberance of bone from the body of the atlas centrum. Whatever were the caudal processes in the development of a dens, selection pressures for its development must have been high once the possibility of rotation at the atlanto-axial joint was realized. A tonguelike or toothlike dens is one of the most invariable features of the mammalian postcranial skeleton. Among modern mammals, only some cetaceans lack a dens.

The dens is unquestionably one of the earliest definitive structures to appear in mammalian phylogeny: Kermack (1963) reported a "fully formed odontoid" in the Late Triassic mammal *Morganucodon.* Kühne (1956) described and figured a dens of mammalian proportions in the Liassic tritylodontid *Oligokyphus.* Although *Oligokyphus* is not a mammalian ancestor, but a specialized and late-surviving therapsid, the morphology of the axis is exactly what would be expected in a mammalian ancestor: the atlas centrum is fused to the axis centrum, as in some cynodonts and in all mammals. But in place of the slight protuberance of cynodonts is a typically mammalian dens. This may be termed the "prototherian" stage in the evolution of the dens and will be now considered with reference to *Ornithorhynchus.*

The final stage in the evolution of the dens is represented by the *Ornithorhynchus* dens, which in morphology and size is entirely mammalian (*d*, Fig. 7). However, the relationship of the dens to the axis centrum is not typically mammalian because these elements are widely separated by a bulbous ossification (C_1, Fig. 7) that bears articular facets for the atlas. In a typical mammalian axis, the dens and cranial articular facets abut against the axis centrum more or less directly beneath the anterior limit of the axis neural arch; the dens and cranial articular facets are not widely separated from the axis centrum. Is the bulbous ossification between dens and axis centrum in *Ornithorhynchus* developed from materials of axis centrum or atlas centrum deriva-

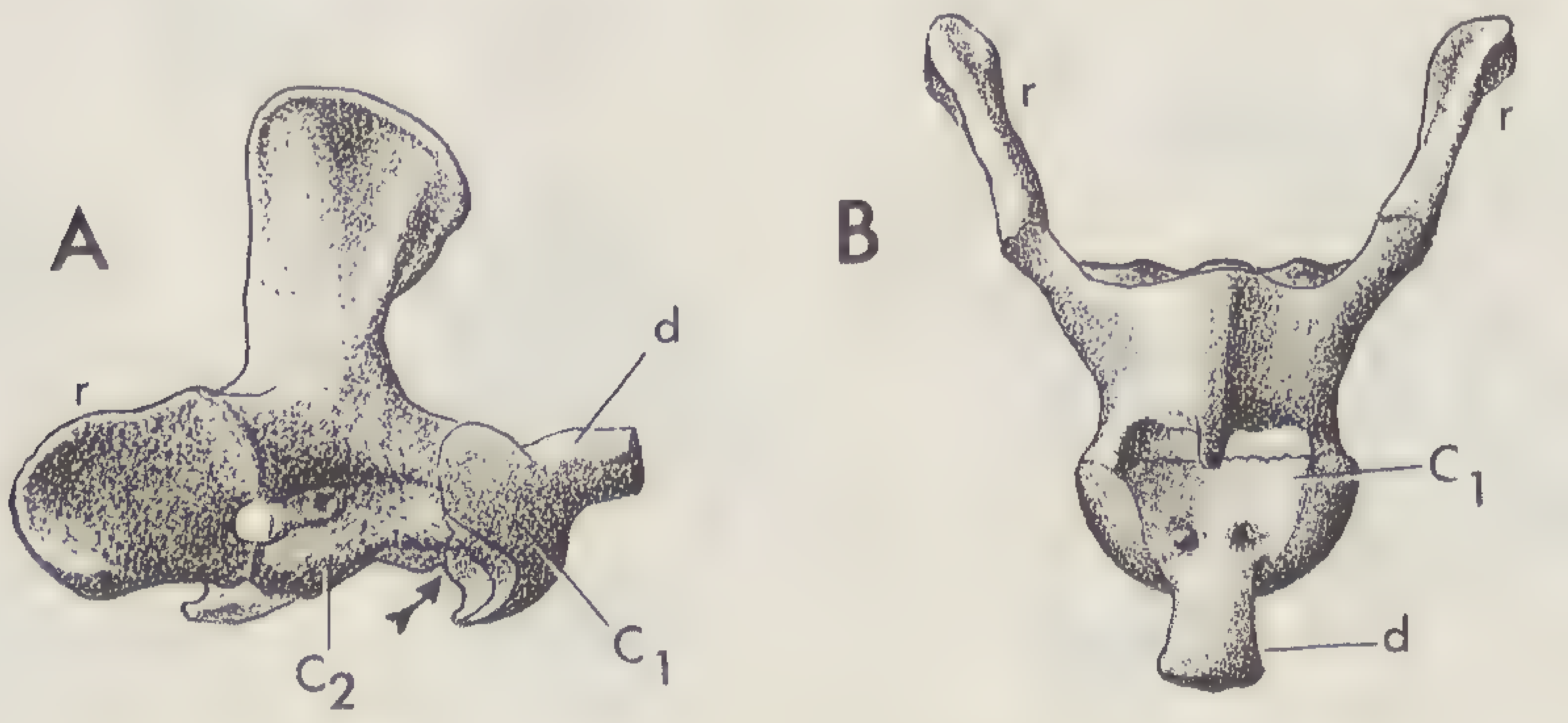

FIG. 7. Axis of a platypus, *Ornithorhynchus anatinus,* YPMOC 5123. A, lateral view; B, dorsal view. Specimen is that of a young adult. Arrow in A indicates the joint between axial and atlantal centra; the same joint can be seen in B running across the floor of the neural canal behind the anterior articular facets for the atlas. X 2. Abbreviations as in FIG. 1 except: *r,* axis rib.

tion? This leads to the crucial question of the homology between the mammalian dens and primitive atlas centrum.

The purported homology between the mammalian dens and the atlas centrum of lower tetrapods was probably first formulated by Cuvier[5]. Among the many workers to investigate the atlas-axis complex, only Ludwig (1954) challenged Cuvier's concept. From serial sections of early human embryos, Ludwig concluded that the dens arose directly from the axis body and that no homologue of the atlas body exists. However, Ludwig's figures show that he misinterpreted his material and that an atlas body is indeed present in humans (Jenkins, 1969: fig. 2F). Kladetzky (1955) gives other criticism of Ludwig's theory. The general acceptance of Cuvier's homology is due to developmental evidence unequivocally demonstrating that the dens is formed from sclerotomic cells in the position expected of the atlas centrum. Heretofore, fossil evidence neither confirmed nor denied this seemingly simple relationship. If Cuvier's homology is taken at face value, then the atlas centrum, originally the diameter of other cervical centra, became progressively smaller during the course of mammalian evolution until only a vestige remained as the peglike dens fused to the axis. In this case the atlas centrum is represented only by the dens. But this view is untenable in face of the evidence that cynodonts possessed both an incipient dens and an atlas centrum of primitive, large size (see above). More important, this view does not account for the origin of the anterior articular facets of the mammalian axis. In both pelycosaurs and cynodonts the posterior facets of the atlas arches articulate only with the atlas centrum. Therefore, there is the possibility that at least the cranial articular facets on the mammalian axis, articulating with the homologues of the atlas arches, represent part of the original atlas centrum. An unknown amount of the supposed axis "centrum" caudal to these facets may also represent the original atlas centrum. No further paleontological evidence is available which supports this hypothesis, but the joints in the axes of recent mammals provide positive confirmation of the presence of part of the primitive atlas centrum posterior to the dens.

In no mammalian axis is there a trace of any joint between the base of the dens and the cranial articular facets, as would be expected if the dens alone were the rudiment of the atlas centrum. In the axis of young mammals, a joint divides the axis transversely and is here interpreted as demarcating the axial and atlantal moieties. This joint, variable in position, apparently closes in early postpartum life. In the monotreme *Ornithorhynchus anatinus* (Fig. 7), the joint lies posterior to the cranial articular facets. With exception of its typically mammalian dens, the *Ornithorhynchus*

[5] Discussing the origin of the concept of a dens-atlas centrum homology (Jenkins, 1969), I believed that Cuvier initially formulated the general idea about 1835 but that Bergmann, Rathke and Owen, among others, were the first to equate the two structures in the sense of homology. Further investigation has revealed that Cuvier made specific deductions concerning the equivalence of the dens and atlas centrum that antedate those of the above mentioned authors, although the term "homology" (with the implication of evolutionary continuity) was not used. In 1808 Cuvier wrote of the crocodilian axis: "A la face antérior du corps, se joint par un cartilage, une pièce convexe à cinq lobes . . . qui tient lieu d'apophyse odontoïde par son lobe moyen. . . ." Cuvier (1824) later made a definitive statement regarding the atlas centrum in turtles: "Cette pièce, analogue à celle que nous avons déjà vue dans le crocodile, représente l'apophyse odontoïde de l'axis des mammifères. . . . Ce qui prouve que cette pièce, analogue à l'odontoïde, est dans le fait le corps de l'atlas."

axis is therefore constituted very much like a cynodont axis. The anterior ossification of *Ornithorhynchus* retains approximately the same anteroposterior length relative to the axis centrum as occurs in the atlas centrum of cynodonts. This anterior ossification, homologous with the body of the atlas, alone bears the cranial articular surface for the atlas as in cynodonts. This surface is composed of two dorsolateral facets, one for each half of the neural arch, and a ventromedial facet for the atlas intercentrum—an arrangement which is essentially the cynodont condition. The monotreme axis is primitive because it retains a relatively extensive articulation between the homologues of the atlas centrum and intercentrum. Typically in more advanced mammals this articulation has been reduced or lost in favor of a new contact between the dens and atlas intercentrum.[6] The primary contact of a metatherian or eutherian axis with the intercentrum ossification is via the ventral surface of the dens which extends dorsally over the intercentral part of the atlas ring. *Ornithorhynchus* and, to a lesser extent, *Tachyglossus* retain both the primitive, ventromedial facet for the atlas intercentrum and the specialized "mammalian" contact via the dens.

In *Tachyglossus aculeatus* (Fig. $8G_1$, G_2) the axis is somewhat more specialized and less cynodont-like than in *Ornithorhynchus*. A small part of the cranial articular facets is borne by the axis neural arches and the ventromedial facet for the (atlantal) intercentral ossification is reduced in size. These incipient specializations are further developed in metatherians and eutherians. Gaupp (1908) studied the development of the atlas-axis complex of *Tachyglossus* in detail. He concluded that the atlas body not only contributed to the formation of the dens, but also to the cranial half of the definitive axis body. His study confirms the present account of the monotreme atlas body forming the major part of the cranial articular facets of the axis—as was the case among cynodonts.

In representative genera of all living families of marsupials, a transverse joint divides the axis body in juveniles. The joint usually occurs entirely posterior to the cranial articular facets, although in a few cases the joint appears to transect the dorsolateral corner of the facets. The joint in marsupials is similar to that in *Ornithorhynchus* or *Tachyglossus* and may be considered as a retention of a primitive condition. However, marsupials share with eutherians the tendency to reduce or lose the ventromedial facet for the atlantal intercentrum (the ventral arch of the atlas ring), so that the ventral surface of the dens is the principle contact of the axis with the ventral atlantal arch. Despite this specialization, marsupials retain a substantial postdens component in the axis that is homologous with the primitive atlas centrum.

The axis of eutherian mammals shows a wide range of morphological variation between orders and even between families. Among juveniles, a transverse joint invariably occurs that separates the dens and a postdens component from the body of the axis. This joint usually transects the cranial articular facets, but not always so as to bisect them. In the dog (Fig. 8D) and Indian elephant (Fig. 8F), the joint divides

[6] In most mammals the atlas intercentrum is represented by a ventromedian center of ossification in the atlas ring. It usually fuses with the two halves of the neural arch to complete the ring but may persist in the adult as a separate ossicle (e.g., *Thylacinus*, see Lessertisseur and Saban, 1967: 586). In some mammals (e.g., *Phascolarctos cinereus*) ossification never occurs and the atlas ring is completed ventrally by a ligamentous band.

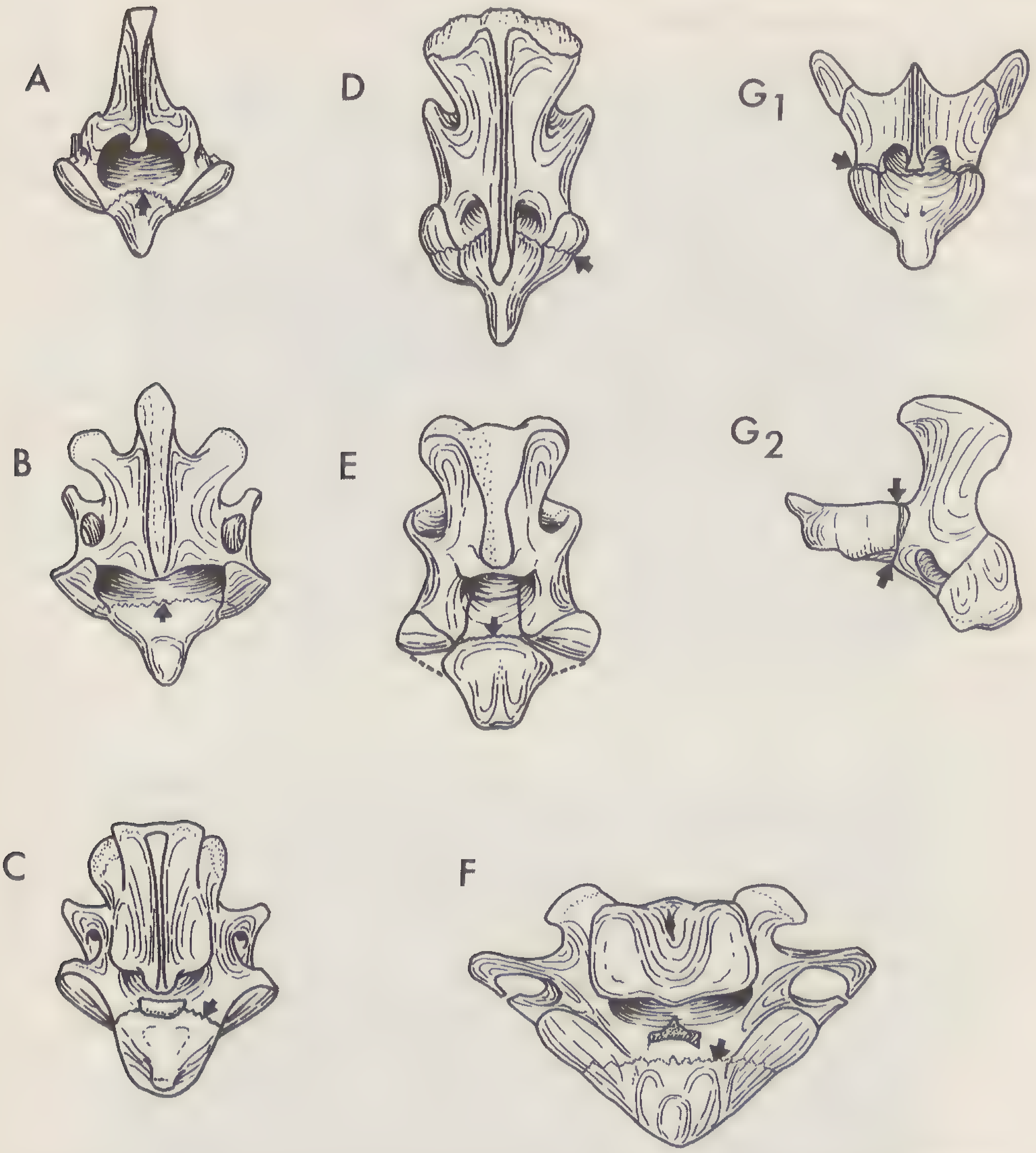

FIG. 8. Axes of juvenile mammals showing the joint (arrow) separating axial and atlantal centra. A, *Dasypus novemcinctus*, YPMOC 2333; B, *Sus scrofa*, YPMOC 1580; C, *Tapirus (Tapirella) bairdi*, YPMOC 287; D, *Canis familiaris*, YPMOC 2600, age 6 months; E, *Equus caballus*, YPMOC 198, age 12 days; F, *Elephas maximus*, YPMOC 210, age approx. 8 months; G_1 and G_2, *Tachyglossus aculeatus*, YPMOC 1691. All dorsal views, except G_2 which is lateral. Not to scale.

these facets approximately in half. In horses (Fig. 8E) and tapirs (Fig. 8C), the joint occurs in a relatively more anterior position, so that the greater part of the cranial articular facets are borne by the axis. The tendency to anterior displacement of the joint or, perhaps, posterior displacement of the facets is even greater in domestic pigs (Fig. 8B), while in some edentates (Fig. 8A) the joint passes entirely anterior to the facets. These examples are sufficient to show that in eutherians there is a considerable range of deviation in joint position from the primitive position posterior to the cranial

facets. More importantly, however, these examples demonstrate that even in the most specialized forms the dens alone is not the sole vestige of the atlas centrum, as is generally believed. A postdens component always occurs. The retention of this component, even in those mammals in which the cranial articular facets are formed entirely from axis elements, relates not only to the phylogenetic history of the mammalian atlas centrum but also to the biomechanical function of the dens (to be considered in the next section).

Among previous workers, W. H. Flower was probably the first to recognize the actual dens-axis relationship. He reported (1885: 35-36) that "if the axis [of a mammal] is examined a year or two after birth, its body appears to be composed of two parts, one placed in front of the other, the first including the odontoid process [dens] and the anterior part of the body, the second all the remainder of the body." Flower drew no further conclusions from this observation, except to note that the posterior extremity of the odontoid ossification represented the "usual disk-like epiphyses of the vertebral bodies." Gadow (1933: 107) objected to these observations on the grounds that Flower "looked upon the odontoid as part of the axis centrum instead of a centrum in its own right. . . ." In fact, Flower did not reject the homology of the odontoid and atlas centrum, but implied, although somewhat indirectly, that more than just the odontoid process was homologous to the atlas centrum. Gadow and others err when they insist that the dens is a "centrum in its own right" that has become reduced in size and fused to the axis. This concept is untenable in view of both the paleontological and recent osteological evidence demonstrating that the dens arises from, and never completely replaces, the atlas centrum, and therefore is properly regarded as a neomorph. Yet authors usually cite unspecified "developmental evidence" to justify the supposed homology, despite the fact that some classical accounts of the subject (e.g., see Froriep, 1886) correctly portray the coexistence of both an atlas centrum and a dens during development. The interpretation of the developmental evidence has been a source of such confusion that it will be reevaluated here, using a marsupial as an example.

The development of the dens in the Virginia opossum, *Didelphis marsupialis*, has been studied with the use of serial sections and osteological preparations of pouch young. The critical question is whether the dens, at any time from its initial differentiation through its completed development, is an entity separate from the posterior ossification noted by Flower (1885) and here identified as the vestige of the atlas centrum. Separate development of the dens could possibly be construed as evidence of its homology with the primitive atlas centrum. Conversely, its development in association with a postdens component would support the paleontological and osteological evidence that it is not strictly homologous with the primitive atlas centrum.

The earliest section available is from a pouch young 20 days postpartum (Fig. 9A). At this stage the completely cartilaginous axis is characterized by two zones of hypertrophied chondrocytes (c_1, c_2). The dens (d) is recognizable as a bulbous excrescence on the anterior of the two zones. From the apex of the developing dens runs a connective tissue strand which later forms the apical ligament. The only feature which distinguishes the dens from the rest of the anterior zone is a slight indentation (*arrow*, Fig. 9A). Otherwise there is no indication at this stage that the dens is developing as an independent structure.

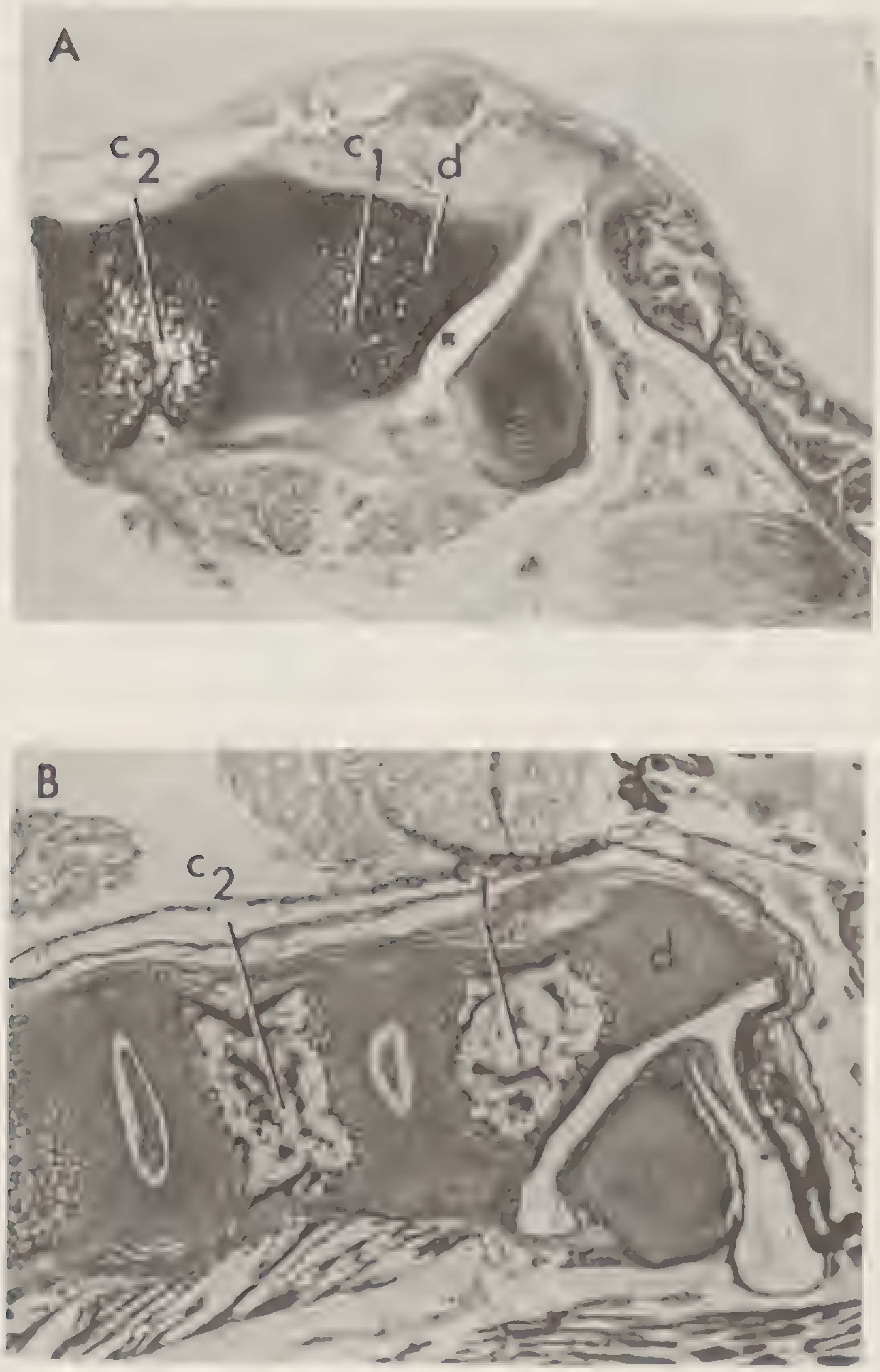

FIG. 9. Sagittal sections through the axes of opposum pouch young (*Didelphis marsupialis*). Upper photograph, 20 days post partum (Wistar Institute Ser. Cat. no. 17683), approx. X35. The two adjacent zones of hypertrophied chondrocytes represent the axis centrum (left) and "atlas centrum" (right). Arrow indicates developing dens. Below and to the right of the arrow is a section through the ventral half of the atlas ring ("atlas intercentrum"). Lower photograph, 25 days post partum, approx. X40. The two adjacent zones of ossification represent the axis centrum (left) and "atlas centrum" (right). The cartilaginous extension of the atlas centrum over the atlas ring represents the dens. For abbreviations see FIG. 1.

The second stage is from a pouch young of about 25 days postpartum (Fig. 9B). The ossifying axis centrum is clearly set off from the centrum of the third cervical vertebra and from an anterior ossification center by the developing intervertebral discs. The dens is still cartilaginous and is developing in conjunction with a large center of ossification (c_1) interpreted as serially homologous with the other ossifying centra. Parasagittal sections show that the dens is the apex of a broad-based, triangular mass of cells, of which the ossification center noted above forms the largest part.

The third and fourth stages are represented by osteological preparations of pouch young estimated to be 50 and 70 days postpartum. In the 50-day-old specimen (Fig. 10A), the axis consists of four unfused ossifications: the two neural arch halves, the axis centrum, and the "atlas centrum" with the dens. The "atlas centrum" (c_1, Fig. 10A) is a triangular ossicle, the blunt apex of which is directed anteriorly. The differentiation of the dens as a peglike, bony structure is just begun. In the 70-day-old specimen (Fig. 10B), the neural arches have nearly completed co-ossification. The axis is not yet ossified to the neural arches nor to the "atlas centrum" ossicle. The dens appears as a process arising from the "atlas centrum" ossicle of which it is a small part.

The fifth and last stage is represented by an osteological preparation of a young adult opossum estimated to be six months old (Fig. 10C). In this specimen the dens is but a small process arising from the "atlas centrum" ossification. This ossification, as in other marsupials, forms the anterior third of the axis body, to include the cranial articular facets. The joint between the "atlas centrum" ossification and the axis centrum is clearly visible.

The developmental history of the opossum dens demonstrates that the dens alone cannot be considered the homologue of the primitive atlas centrum, as is so often implied or stated. It is indisputable that the dens originates in conjunction with an embryonic structure, the so-called "atlas centrum" ossicle, which is homologous in position with the atlas centrum anlage of primitive tetrapods. Beyond this, it is useless to attempt to apply the concept of homology. The atlas centrum of mammals has been re-cast, so to speak, so that the dens is most appropriately regarded as a neomorph.

The Function of the Dens

The functional importance of the dens is its adaptation to maintaining the integrity of the atlanto-axial joint. Most authors state that the dens acts as an "axis" or pivot about which the atlas rotates, but this function is of secondary importance. The atlas can and does rotate in the absence of a dens or in cases where the dens is congenitally separate from the axis. However, in such cases the joint is weakened and the possibility of atlanto-axial dislocation increased. The stabilizing function of the dens in the atlanto-axial joint is correlated with the loss of the atlanto-axial zygapophyses, which is necessary to permit rotation (see below, p. 41).

Rockwell, Evans and Pheasant (1938: 104) and Slijper (1946: 118) show that the basic mechanics involved in the suspension of the head and neck are those of a loaded beam that is supported at one end only. The centra may be considered as

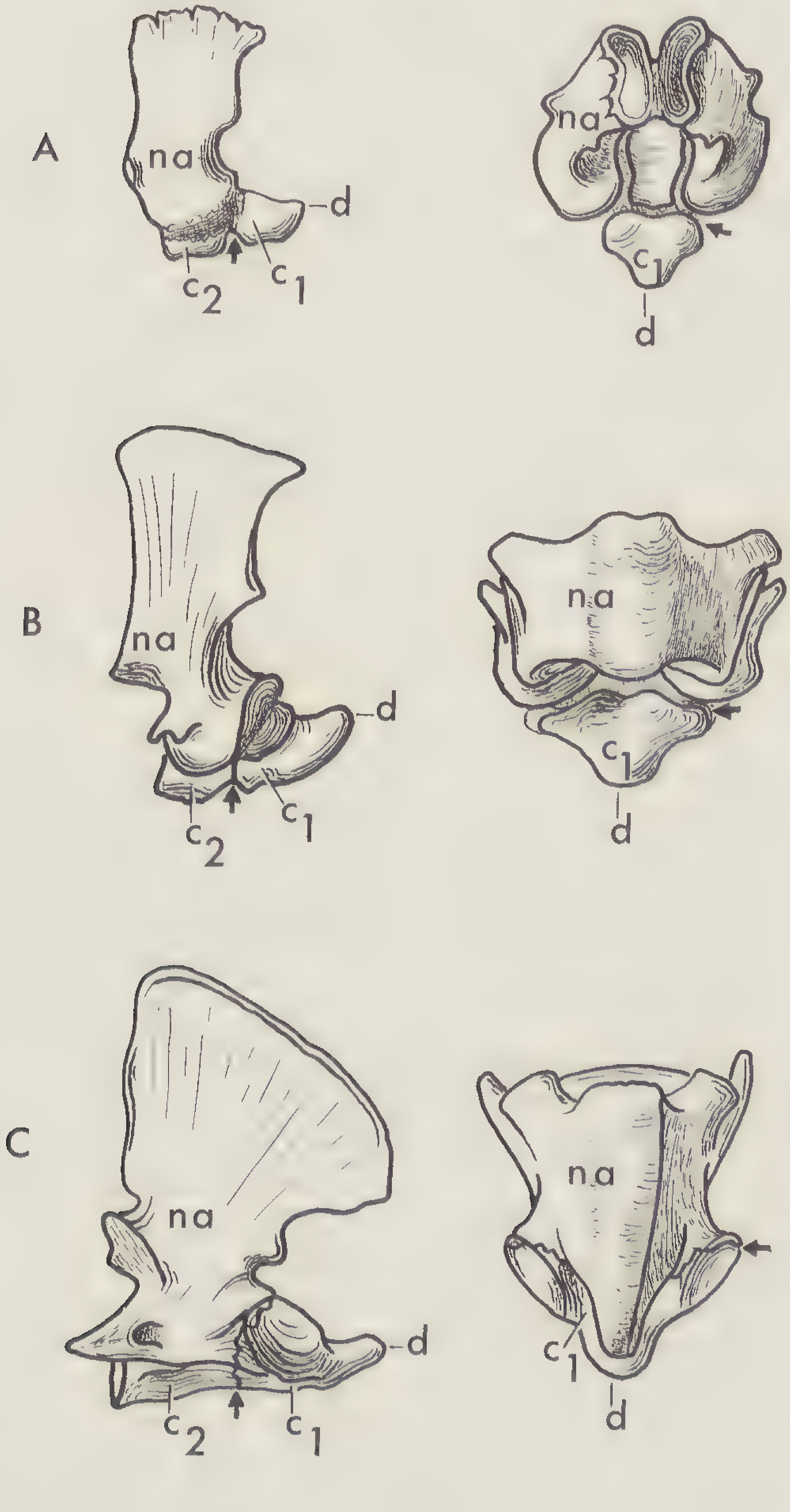

FIG. 10. The development of ossification of the axis in the opossum (*Didelphis marsupialis*). Left, lateral views; right, dorsal views. A, pouch young opossum, YPMOC 5502, estimated to be 50 days post partum. Approx. X5.25. B, pouch young opossum, YPMOC 5331, estimated to be 70 days post partum. Approx. X5.25. C, young adult opossum, YPMOC 243. Approx. X1.9. Arrow indicates joint between axial and atlantal centra. For abbreviations see FIG. 1.

compression-resisting members, and the neural arches, their processes, associated ligaments and muscles as tension-resisting members. With the loss of the atlanto-axial zygapophyses, this joint loses a critical tension-resisting mechanism. The weight of the head, which tends to flex the cervical series, therefore places a disproportionate amount of stress on the atlanto-axial joint relative to other cervical joints. To offset this structural weakness, several adaptations are possible. First, fusion of the atlas arches with the development of a dorsal atlanto-axial ligament replaces in some degree the lost zygapophyseal bond. But the ligament cannot be so extensive and taut that it interferes with the freedom of rotation; therefore, the ligament does not substitute for the zygapophyses, and the joint must be strengthened elsewhere.

A second possible adaptation is to increase the radius of curvature of the articulating atlanto-axial facets, resulting in a ball-and-socket joint. *Ornithorhynchus* (Fig. 7) shows the partial development of such a specialization. Yet this specialization is not common in mammals because it fails to balance completely the mechanical disadvantage engendered by the loss of zygapophyses. A ball-and-socket joint, in order to withstand the flexion stresses generated by the weight of the head, must be reinforced by strong ligaments along its dorsal margin. Such ligaments would also restrict the rotation of the joint, and hence nullify the rotational advantage gained by loss of the zygapophyses. In most mammals the atlanto-axial articulation is in fact shallow, with no indication of this type of specialization.

A third possible adaptation is to strengthen the atlanto-axial joint along its principal axis of movement, i.e., with a dens and its associated ligaments. These structures do not inhibit rotation because they reinforce the joint along the axis of rotation. The exceptions are the alar ligaments of the dens. However, these ligaments, which pass from the apex of the dens to the medial side of each condyle, are apparently important in the restriction of extreme rotational movement. (The other adaptations mentioned above reinforce the joint peripheral to its axis of rotation, and therefore tend to restrict rotation.) The functionally most important ligament with regard to the dens is the transverse ligament of the atlas (ligamentum transversum atlantis). This ligament passes from one side of the atlas arch to the other and divides the space for the dens below from the neural canal above. A synovial bursa between the dens and the transverse ligament facilitates rotation of the dens but does not interfere with the function of the ligament. This function, as generally recognized (Miller, et al., 1964: 103; Gray, H., 1959: 333), is to hold the dens against the ventral arch of the atlas. Acting together, however, the dens and transverse ligament prevent the atlas (and head) from flexing on the axis. The elongation of the dens and its retention by a transverse ligament anterior to the atlanto-axial facets is a simple mechanism for maintaining the strength of an intervertebral articulation without compromising rotational ability. The mammalian atlanto-axial joint without the dens and transverse ligament would be no less mechanically suited for rotation; it would lack, however, the mechanical means (musculature not considered) to sustain the stresses generated by the movements and particularly the weight of the head. The transverse ligament, as well as the apical and alar ligaments of the dens, maintains the integrity of a joint otherwise specialized to permit a very wide range of movement. In horses and in some ruminants (cow, sheep) the transverse ligament is negligible or absent (Barone and Lombard, 1967). However, in these forms functional replacements of the transverse ligament exist ("odontoid liga-

ment"; "pseudo-alar ligaments") so that the mechanical role of the dens appears to be essentially unchanged.

Independent evolution of a dens and transverse ligament has apparently occured in birds. Possibly living reptiles have also independently evolved a dens or pseudo-dens complex. As Cuvier (1808) first observed, crocodiles typically have a short, median tubercle occupying a dorsal position on the anterior aspect of the dens, a position which Cuvier correctly noted was that of an odontoid process (true dens). Hoffstetter and Gasc (1969) figured atlas centra of certain lizards, snakes and amphisbaenids that likewise bear an anteriorly directed tubercle or eminence occupying a dens-like position; these authors, apparently ignoring this process, referred to the entire atlas centrum as the odontoid process. The studies of Gaupp (1908) and Williams (1959) revealed that the reptilian altas-axis joint possesses a number of bony and ligamentous similarities to the dens complex of mammals. To what extent the reptilian arrangement functionally parallels that in mammals is presently a moot point, but in no case should the terms odontoid process or dens be applied to the whole of the reptilian atlas centrum.

The Evolution of Atlanto-Axial Rotation

In pelycosaurs the possibility of atlanto-axial rotation is strictly limited by the nearly vertical zygapophyseal articulations (*pre z*, Fig. 6B) and by the posteriorly directed spine arising from the lateral surface of the atlantal postzygapophysis (*s a a*, Fig. 6A; see Romer and Price, 1940: 108). In cynodonts the zygapophyses of the axis are much reduced in size (*pre z*, Fig. 2A; see also the *Diademodon*(?) axis figured by Brink, 1955: 23) and the atlas postzygapophyses are altogether absent as distinct processes (see above). Therefore the possibility of rotation did exist, but it must have been limited because the articulating facets of the atlas neural arch and centrum are of approximately the same size. As a general rule, there is a disparity in the area of apposing facets when the joint permits a significant amount of sliding movement. In the atlanto-axial joint of the dog, for example, the axial facet extends dorsally beyond the atlantal facet on both sides. The extension allows continuous contact of articular cartilage as the atlas rotates.

Virchow (1914) demonstrated that one function of zygapophyses is to prevent intervertebral rotation. The evolution of the ability of the skull and atlas to rotate about the atlas centrum presupposes modification and eventual loss of the synovial joints of the atlanto-axial zygapophyses. In cynodonts the ventral aspect of the atlantal laminae lay across the dorsolateral surface of the vestigial axial prezygapophyses (Fig. 3B, C). Apparently the relationship between the two was analogous to a shelf (the atlantal laminae) supported by pegs (the vestigial axial prezygapophyses). However there are no distinct facets on the ventral surface of the laminae that would indicate the presence of a synovial capsule between the laminae and axial prezygapophyses. Therefore it is possible that the original synovial capsules were already replaced by a simple ligamentous connection. Whether the atlanto-axial "zygapophyseal" articulation in cynodonts was synovial or ligamentous, there is no question that this region is much modified from the primitive condition. The reduction and eventual loss of the primitive synovial capsule in this region is significant because of

certain functional limitations that it imposed upon the joint. Zygapophyses are usually points of hinge-type movement; that is, the axis of movement is perpendicular to the facet surface at its center. Specialization (e.g., in crocodiles) often allows some sliding or gliding movement but such is probably limited to a relatively small excursion by the articular capsules which enclose them. Mammals, therefore, lose the atlanto-axial zygapophyseal articulation and specialize the atlanto-axial joint for rotation of the atlas neural arches and intercentrum about the atlas centrum. The supporting function of the lost zygapophyseal joints is replaced largely by the dens and its associated ligaments, by the ligamentum flavum and by the dorsal atlanto-axial ligament (e.g., in the dog, Miller, et al., 1964: 102, 104). Cynodonts represent an important phase in the transition to a mammalian atlanto-axial joint because the axial prezygapophyses no longer present any bony restriction to movement of the altantal arches.

The specialization of the mammalian atlanto-occipital and atlanto-axial joints is characterized by the tendency toward separation of the synovial capsules of one joint from the other. In cynodonts each half of the atlas neural arch bears two facets, one for the atlas centrum, the other for the occipital condyle (*f a c*, *f o c*, Fig. 1A). The two facets of a neural arch half are more or less confluent and are invariably covered by smooth, laminar bone. There is no evidence to indicate that these facets were divided by any sort of membrane. In all probability both facet surfaces were enclosed by a single "cervico-occipital" joint capsule. In this respect the cynodonts, despite their bicondylic condition, represent no advance over the pelycosaur condition. The separation of the "cervico-occipital" joint capsules into discrete atlanto-occipital and atlanto-axial capsules took place during a post-cynodont stage of evolution. This specialization is evidently related to a degree of joint movement which cynodonts had not yet achieved.

The second, or atlanto-axial, intervertebral foramen of most mammals is enlarged relative to other cervical intervertebral foramina. The evolution of atlanto-axial rotation apparently has necessitated this relative enlargement to prevent constriction of the second spinal nerve and associated vessels during normal movement. Spinal nerves and vessels caudal to the second cervical nerve are not subject to interference from the intervertebral foramina because the relative amount of movement between vertebrae is small. However the caudal intervertebral notch of the rotating atlas is considerably displaced relative to the cranial intervertebral notch of the axis. By offsetting the two halves of the atlanto-axial intervertebral foramen, rotary movement would damage the nerve and vessels if the foramen were not enlarged sufficiently to remain open despite rotation. Atlanto-axial rotation in living reptiles is apparently so slight that the nerve and vessels are not endangered; the atlanto-axial intervertebral foramen is comparable in size to those adjoining it. It is interesting that in pelycosaurs, which could not have had atlanto-axial rotation (see above), the atlanto-axial intervertebral foramen is comparable in size to others in the cervical series. Yet in cynodonts, where the reduction of the atlanto-axial zygapophyses allows the possibility of rotation, the atlanto-axial intervertebral foramen is markedly increased in size relative to other foramina (Fig. 3B). It is therefore likely that cynodonts did possess the ability to rotate the skull, atlas arches and intercentrum to some degree about the atlas centrum.

The ability of mammals to rotate the head and atlas about the dens of the axis is as much dependent upon specializations of musculature as it is upon specializations of

joints and ligaments. Evans (1939: 54, 74–75) summarized the occipital and cervical musculature of representative reptiles and mammals. All three of the major systems of reptilian epaxial muscles—iliocostalis, longissimus, and transversospinalis—are also represented in the mammalian neck. The functional difference between the two classes probably lies in the greater amount of muscular specialization in mammals. This specialization may be manifested by regional differentiation, e.g., the semispinalis capitis into a biventer and complexus, or by partial reduction, e.g., the iliocostalis typically confined to the posterior cervicals. Nevertheless, both reptiles and mammals have evolved such a diversity of specializations that it is outside the scope of this work to attempt a thorough functional comparison. One major and consistent difference, however, occurs in the transversospinalis musculature between the occiput and atlas-axis and concerns rotation at the atlanto-occipital joint. In reptiles an M. obliquus capitis magnus originates on the axial spine and atlantal neural arch and inserts on the occiput; a small M. obliquus capitis minor[7] passes from the neural arch of the axis to the atlantal postzygapophyses (Evans, 1939: 54). In mammals these muscles are absent. In their place is an M. obliquus capitis cranialis (or superioris) passing from the wing of the atlas to the occiput and an M. obliquus capitis caudalis (or inferioris) originating on the spine of the axis and inserting onto the wing of the atlas. As an extensor of the atlanto-occipital joint, the obliquus capitis cranialis is a functional analogue of the reptilian obliquus capitis magnus. The obliquus capitis caudalis is primarily responsible for rotating the atlas and head about the dens of the axis and has no functional analogue of comparable efficiency in reptiles.

Distinct osteological modifications of the atlas and axis have evolved in conjunction with the mammalian obliquus muscles. Some of these are explicable in terms of increasing the efficiency of rotatory movement. One prerequisite of vertebral rotation is that the effecting muscle fibers must have a substantial transverse component in contrast to the typically longitudinal component of median epaxial muscles. In mammals this is accomplished by localization of rotational movement between two vertebrae, thus reducing to a minimum the longitudinal component of intervertebral muscles. The transverse component of these muscles is further increased by extending the atlas wing laterally and posteriorly, so that inserting fibers arising from the axis spine pass more directly laterally. Concomitantly, the length of the ossification representing the atlas centrum is reduced, with the result that the cranial articular facets of the axis impinge upon the joint which represents the union of the primitive atlantal and axial centra. Rotational efficiency is obviously increased by bringing the atlas ring as closely beneath and therefore lateral to the axis spine as is mechanically possible. The axis centrum of pelycosaurs and cynodonts, being of almost normal length, bears the atlas arch facets well ahead of the axis spine. This primitive condition is inherited by the monotremes. But in other mammals the same facets have migrated posteriorly; this displacement, together with the forward extension of the axis spine, results in an effective rotational component for the obliquus capitis caudalis.

In living reptiles (e.g., *Iguana, Sphenodon*), rotation probably occurs both at the atlanto-occipital and atlanto-axial joints, with the greatest amount of rotation at the

[7] Evans (1939) termed this muscle obliquus capitis inferior which duplicates the name of another muscle in mammals of entirely different attachment and function.

former (see Evans, 1939). The prime movers in rotation are the Mm. obliquus capitus magnus and minor. In neither of these muscles is the lateral component as large as in mammals, i.e., with muscle fibers oriented at an angle of more than 45° away from the longitudinal spinal axis. The obliquus capitis magnus is the more oblique of the two, but its lateral component is reduced by virtue of passing some distance anteriorly over the atlas before inserting on the occiput.

Before discussing atlanto-axial musculature in cynodonts, a critical evaluation must be made of the important contribution of Evans (1939) on the evolution of the atlas-axis from fish to mammals. In discussing cynodonts, Evans used *Galesaurus* and *Cynognathus* as prototypes; his conclusions were not based on original material, but rather on the descriptions of Parrington (1934) and Seeley (1895b). Evans (1939: 68) concluded that cynodont atlanto-axial "muscles, in keeping with the mammal-like character of the occiput, the atlas neural arch and transverse process, and the spinous process of the axis, were probably similar to those of a primitive animal such as the opossum." Evans' reconstruction (his fig. 11) of the muscles surrounding the atlas-axis of *Galesaurus* therefore shows the mammalian Mm. obliquus capitis cranialis and caudalis rather than the reptilian Mm. obliquus capitis magnus and minor. Evans' use of *Didelphis marsupialis* as a model for reconstructing cynodont occipital musculature is disputable on several grounds. First, the "mammal-like character" of the cynodont occiput to which Evans alluded does not necessarily indicate a mammalian arrangement of atlanto-axial musculature. I have examined several acid prepared galesaurid skulls and could find no muscle scars to support Evans' interpretation. Second, I cannot determine what features of the cynodont occiput that Evans recognized as exclusively mammalian. It is possible that Evans recognized a basic similarity in form and outline between the cynodont and generalized mammalian occiput, but these common characteristics are probably as much related to brain and jaw musculature requirements as occipital musculature. Occipital form is thus not solely determined by epaxial musculature. It is also possible that Evans interpreted the relative expansion of the cynodont occiput as similar to that in mammals; however, the occiput in pelycosaurs and even in cotylosaurs is a relatively broad surface and per se does not indicate a mammalian arrangement of musculature. In my opinion the cynodont occiput provides no evidence of a mammalian arrangement of atlanto-axial muscles.

Evans also claimed that the atlas neural arch and transverse process are mammal-like. The atlas neural arches, with the exception of the loss of postzygapophyses, are hardly more advanced than in pelycosaurs. The important step towards the mammalian condition—fusion of the laminae—has not occurred. As for the atlas transverse processes, Evans' figure shows them to be comparable in morphology and orientation to those of the third cervical vertebra. In fact the orientation of the atlas transverse processes, being nearly vertical, is different from that of the axis transverse processes (Fig. 3B). This feature is particularly difficult to account for in terms of a mammalian arrangement of musculature because in mammals the atlas wing tends to a more horizontal than vertical orientation. Therefore the cynodont transverse process is not prima facie evidence for a mammalian arrangement of obliquus muscles.

Finally, Evans cited the mammal-like character of the axis spine as evidence for his reconstruction of the muscles. However, it is difficult to define "the mammalian type"

of axis spine in view of its wide range of morphological variation (see Lessertisseur and Saban, 1967: 607). In general, mammalian axial spines are elongate, flared laterally along their posterior margin, and bear a rather deep spinous fossa on the lateral surface. But the reptilian axis spinous process is also commonly elongate (Hoffstetter and Gasc, 1969) and comparable in shape to that in mammals. The common diminution or absence of a well-developed spinous fossa in the reptilian axis is correlated, in part, with the lack of expansion of the posterior margin of the spine. In cynodonts the spine is elongate (but little more so than in pelycosaurs; compare Figs. 2A and 6A); the spinous fossa is incipient; and the expansion of the posterior margin is negligible. There is no clearly defined aspect of the spinal morphology indicating that its associated obliquus muscles were of a mammalian arrangement.

Nowhere in Evans' analysis does there appear to be any cogent evidence for modeling a reconstruction of cynodont atlanto-axial musculature after a mammalian pattern. However, Evans (1939: 91) did outline how the arrangement of obliquus muscles of mammals might have been derived from the reptilian pattern. His theory is credible, but since it cannot be linked with any fossil evidence it is also purely speculative. The question of the exact disposition of obliquus muscles in cynodonts at present has no satisfactory solution, but it is a less important question once the functional aspects of the joint are recognized.

The significant aspects of cynodont anatomy with respect to atlanto-axial rotation are: 1) that the reduction of atlanto-axial zygapophyses removes any osteological obstruction to rotation; 2) that the orientation of the atlas transverse process is different from other cervical transverse processes, which is evidence for incipient specialization of the associated musculature, possibly for rotation; and 3) that the atlanto-axial intervertebral foramen is enlarged, a feature which is correlated in mammals with the prevention of spinal nerve and vessel occlusion during rotation. In these features cynodonts represent an advance over pelycosaurs in which the zygapophyses prohibit atlanto-axial rotation and in which the atlas transverse process and atlanto-axial intervertebral foramen are similar to others in the cervical series. Undoubtedly the atlas-axis relationship of cynodonts represents an initial phase in the evolution of a rotational joint. But in cynodonts it had obviously not attained the functional efficiency which has so narrowly canalized the morphology of this joint in mammals. Evans (1939: 68) erred when he compared the axis of *Cynognathus* with that of *Tachyglossus*, concluding that the atlanto-axial movements—"chiefly abduction and a slight rotation"—were the same. Monotremes, in fact, have already achieved a mammalian type of specialization for rotation, including a well-developed dens and a typical atlas wing. In addition, they possess an ability of atlanto-axial abduction that probably was never developed in other mammals. This ability, as Evans notes, is due to the posterolateral extension of the axial facets for the atlas. It appears to be a specialization and perhaps is related to another specialization—the loss of all cervical zygapophyseal articulations. In cynodonts the ability to abduct could not have been very much developed because the apposing axis and atlas facets are of approximately the same size. In addition, the atlas laminae would have contacted the adjacent axis arch during abduction. The available evidence leads to the conclusion that atlanto-axial movement in cynodonts was restricted to a small amount of rotation.

Evolution of Atlanto-Occipital Flexion and Extension

The bicondylic atlanto-occipital joint of mammals is particularly specialized for flexion and extension. In *Didelphis*, for example, the flexion-extension arc is approximately 90°. In most, if not all, mammals the articulation also permits a small degree of abduction because the joint surfaces, viewed from above, represent arcs of a relatively large circle. Neither flexion-extension nor abduction at the atlanto-occipital joint are mammalian innovations, for both were undoubtedly present in synapsid and even in more primitive reptiles. The feature that characterizes the mammalian atlanto-occipital joint is the substantial increase in the flexion-extension arc. The starting point in its evolution is among pelycosaurs; they lacked any such specialization but reveal the basic plan from which it was developed. The mammalian specialization that permit the extensive range of movements will be defined before cynodont anatomy is evaluated as a stage in their development.

The phylogenetic history of the mammalian atlanto-axial joint has demonstrated the principle that specializations for greater freedom of movement evolve concomitantly with specializations for increased control and for maintaining the strength of the joint. In the pelycosaurian atlanto-occipital joint the joint surfaces (excluding the proatlas) are in size comparable to the intercentral articulations of postaxis vertebrae. In terms of structural elements the atlanto-occipital joint represents a slightly modified intercentral articulation. The joint itself is rather shallow (Fig. 11A), a feature which undoubtedly permitted a certain amount of freedom but which could not contribute to its strength. Thus the pelycosaurian atlanto-occipital joint sacrifices some strength for mobility and the inherent weakness must be compensated for elsewhere. The critical stresses at the atlanto-occipital joint are produced by the weight of the head. The forces generated, as noted before (p. 38), are those of compression along the ventral half of the spinal column, i.e., between centra, and tension along the dorsal half, i.e., between neural arches and zygapophyses. A shallow atlanto-occipital joint may adequately accommodate compressive forces between the condyle and the atlas, but it is not suited to resist tensile forces, i.e., the tendency to atlanto-occipital flexion or separation induced by the weight of the head. Hence an additional element is required—the proatlas—analogous in function to the zygapophyses of other cervical vertebrae. The important functional difference between cervical zygapophyses and the proatlas is that the former have only one joint capsule to a side whereas the latter, articulating with both the atlas neural arch and occiput, has two. The proatlas ossification provides a tension-resisting element, while the fact that it has two joint capsules allows more latitude for movement than would be possible at one capsule. Nevertheless the proatlas essentially restricts both flexion and extension.

In mammals the proatlas is absent or, rather, does not ossify separately. The ventral half of the "pro-atlantal" sclerotomite forms the apex of the dens (see below). The dorsal half, which in certain reptiles ossifies as the proatlas, apparently has a variable role in mammalian development. Hayek (1923; 1927: 276–278) claimed that in man, moles, rabbits and other mammals the proatlas arch anlage contributes to the formation of the occipital condyles, an observation which has been repeated for

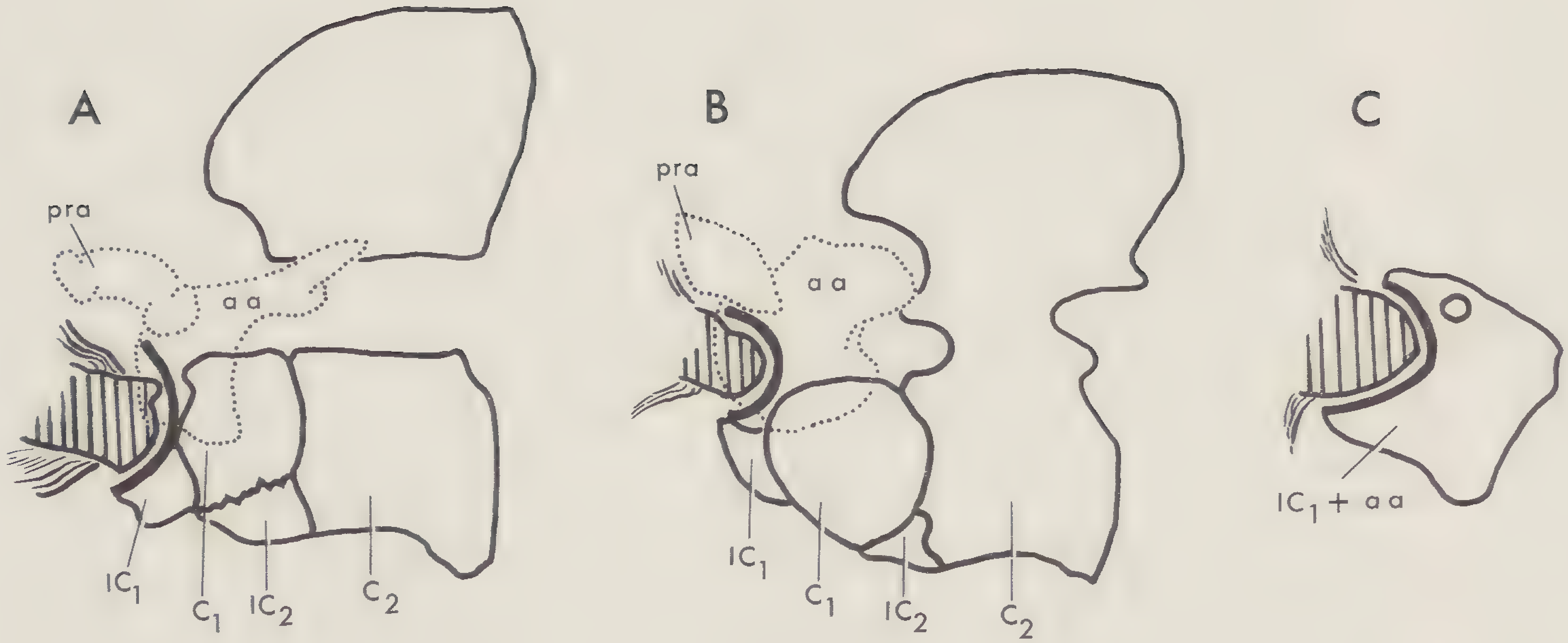

FIG. 11. A, reconstructed sagittal section through the atlanto-occipital joint of a pelycosaur. The same for B, a cynodont, and C, a dog, except that these sections are parasagittal because the condyles are located lateral to the sagittal plane. Heavy line indicates the relative depths of the atlanto-occipital joints. Dotted line traces the outline of the atlas, neural arch, and proatlas in the pelycosaur and cynodont. Not to scale.

human embryos more recently by Ingelmark (1947) and Sensenig (1957). The latter author also claimed that the proatlas arch contributes to the formation of alar and other ligaments of the atlanto-occipital joint. However, Barge (1918) found that in sheep the neural arch half of the "pro-atlantal" sclerotomite joins with the atlas and Sensenig (1943: 133) confirmed the same condition in *Peromyscus*. Apparently the lack of separate ossification of the proatlas in mammals permits its anlage to follow a variety of developmental courses.

The absence of a proatlas in mammals is probably correlated with the increase in the flexion-extension arc. However the loss of the proatlas alone does not account for the substantial increase in the flexion-extension arc. Since the proatlas primarily strengthens the atlanto-occipital joint, its loss requires compensatory adaptations which will maintain the strength of the joint and at the same time permit considerable latitude in flexion and extension. The two most important adaptations are therefore interrelated: the doubling of the condyles and the decrease in their radius of curvature. Doubling the condyles provides potentially a greater amount of articular surface and, hence, strength to the joint. However a large, broadly curved articular surface as in pelycosaurs is an inefficient hinge for flexion and extension. Such a surface engenders more displacement of the occiput per degree of flexion than a sharply curved surface. The mammalian double condyle provides both the larger area of articular surface for a stronger joint and the smaller radius of condylar curvature to facilitate flexion-extension (Fig. 11C). In addition, the dorsal margins of the occipital facets of the atlas are commonly reflected ventrally (Lessertisseur and Saban, 1967: 602), thus extending the facet surface and at the same time tending to encircle the condyles. The condyles themselves become hemicylindrical and, more importantly, their ventral surfaces are extended anteromedially to provide facet area for maximum flexion. Furthermore the development of lateral atlanto-occipital ligaments (e.g., in the dog, see Miller, et al., 1964: 101; or in the horse, see Sisson and Grossman, 1953: 217) reinforces the joint yet does not interfere with flexion or extension because these ligaments approximately coincide with the transverse axis of movement. The mammalian atlanto-axial joint thus combines features that permit an increased degree of flexion and extension but that also are adapted to transmitting the stresses of head weight.

The cynodont atlanto-occipital joint shows significant advances over the pelycosaurian condition with regard to increasing the flexion-extension arc (Fig. 11B). Most cynodonts are truly biocondylic and have eliminated the possibility of atlanto-occipital rotation present in pelycosaurs. In this sense, cynodonts have begun to specialize the joint for flexion and extension; by doubling the condyles the relative amount of articular surface is increased and the radius of condylar curvature is also increased. The anterior neural arch facet for the occipital condyle is anteroposteriorly longer than the adjoining facet for the atlas centrum, which is the reverse of the pelycosaurian condition. Nevertheless the atlantal facets for the occipital condyles are still comparatively shallow. The articular cartilage of the atlas, supported by three independent elements, intercentrum, neural arch and centrum, could not form as strong an articular capsule as in the mammalian atlas where these elements are fused. Extension was almost centainly limited by the intercalation of the proatlas between arch and occiput. The proatlas also probably restricted flexion; the lack of any significant ventral extension of the condylar facets is corroborative evidence. The possibility that

cynodonts possessed a greater flexion-extension arc than pelycosaurs appears likely on evidence of the doubling of condyles. Nevertheless cynodonts retained many features of a pelycosaurian grade and lacked the mechanical refinements which are so characteristic of the mammalian arrangement.

3. THE POSTCRANIAL AXIAL SKELETON OF *THRINAXODON*

MATERIAL. A nearly complete, articulated axial skeleton of *Thrinaxodon* cf. *liorhinus* (AMMM 5265) is described below. The matrix was removed by acid, revealing most of the minute details. The specimen is for the most part undistorted. Missing are most of the cervical ribs, the distal ends of most thoracic ribs, and the caudal vertebrae. The atlas-axis complex is incomplete and damaged, but this is well known from other specimens. Other small breaks in the neural spines and costal plates aside, this specimen as preserved represents the most perfect of known cynodont axial skeletons.

Numerous other *Thrinaxodon* axial skeletons, most of them incomplete, damaged during preparation, or incompletely prepared, were studied as additional reference material. Among the more important of these specimens are those in the National Museum (Bloemfontein, Republic of South Africa) collection, originally described by Brink (1954). Others include AMNH 2228, USNM 22812, BPI 287 and BPI 376. However, unless otherwise specifically cited by number, the following description is based on AMMM 5265.

Cervical Series

MORPHOLOGY. The number of cervical vertebrae in *Thrinaxodon* is of interest to compare with the almost invariable mammalian number of seven. The determination of the number is complicated by the fact that *Thrinaxodon*, unlike most mammals, retained cervical ribs, the absence of which is a primary feature of mammalian cervical vertebrae. Brink (1954: 117) described *Thrinaxodon liorhinus* (NMB C.392) as having five cervical vertebrae. Brink's division between the cervical and thoracic series was based apparently on his observation that the "first thoracic vertebrae [*sic*] has the tallest dorsal process." Re-examination of this specimen shows that in fact the heights of the neural spines on the fifth, sixth and seventh vertebrae are subequal and that the state of preparation prohibits a confident estimate as to which, if any one, is the highest. Two acid-prepared specimens of *Thrinaxodon* (SAM R.377, SAM uncatalogued), if considered together, show that the spine of the seventh vertebra is slightly taller than any preceding spine. Brink (1954: fig. 2) restored the seventh and eighth neural spine of *Thrinaxodon* as the tallest, which is probably correct. A clearly defined morphological division is evident in AMMM 5265 between the seventh and eighth vertebrae; as will be documented more fully below, this transition involves a shift in orientation

of the zygapophyses and transverse processes and a change in the morphology of the neural spines. The same morphological changes are consistently developed in other specimens and therefore I conclude that *Thrinaxodon* has seven and not five cervical vertebrae.

Intercentra occur as single, crescentic ossicles interposed ventrally between successive pleurocentra; their width is approximately one half the width of the adjacent pleurocentra. In AMMM 5265, intercentra are preserved between the first five centra (IC_1, IC_2, etc., Fig. 12B, C); from the appearance of the beveling along the adjacent ventral margins of the fifth, sixth and seventh cervical vertebrae, intercentra probably occurred here also. An intercentrum possibly occurred between the last cervical and first thoracic, but caudal to this point intercentra are certainly absent.

Pleurocentra are deeply amphicoelous, approximately circular in cross-section and slightly constricted laterally and ventrally around the middle. Facets for the rib head occur as clefts between adjacent centra; each cleft is formed by two opposed facets obliquely beveled into the dorsolateral aspect of the rims of adjacent centra (*f cap*, Figs. 12C, 13A).

Pedicles join the body along an irregular suture. Anteriorly, each pedicle forms a protruding lip which overhangs the rim of the centrum and thus participates in the intervertebral articulation; functionally, the protruding pedicle lips may have served to inhibit dorsal displacement of an anterior relative to a posterior vertebra. The pedicles are indented anteriorly and posteriorly to form cranial and caudal vertebral notches of which the former is invariably the most deeply incised. The intervertebral foramen thus formed is bordered dorsally by a posteriorly directed anapophysis received into a lateral depression of the next posterior pedicle (*ap*, Figs. 3B, 12C). This lateral depression occurs directly dorsal to the cranial vertebral notch and lies directly ventral to the prezygapophysis.

Anapophyses arise ventrolaterally to the postzygapophyses as elongate, blunt eminences which are smoothly convex laterally but which are flattened medially to conform with the lateral depression of the following pedicle. Anapophyses diminish in size anteriorly and do not occur on the atlas.

The pedicles bear stout transverse processes, diapophyses, which are directed posterolaterally and ventrally on the axis and on the third through the sixth cervical vertebrae (*tr p*, Figs. 3, 12). The transverse processes of the seventh cervical are the most slender and project laterally; on the first thoracic vertebra, they project anterolaterally. The facets for the tuberculum also show a morphological gradient. On the axis the facet is an elongate oval, the long axis of which is directed anteroventrally ($tr\ p_2$, Fig. 3A–C; in Fig. 12C, the left half of the axis arch is lost; in Fig. 12B, the right transverse process is obscured by its rib). On the posterior cervicals the facet becomes successively less elongate and its long axis more vertically oriented, so that at C_7 the facet is nearly round with a slight ventral projection from its anteroventral corner. This projection becomes successively more developed in the thoracic series until the tubercular and capitular facets are continuous and form a synapophysis.

The angle of zygapophyseal articulation increases from an angle of approximately 45° to the horizontal between the axis and third cervical vertebra to an angle of about 55° between the sixth and seventh cervical vertebrae. The laminae that bear the zygapophyses decrease in breadth from 7.3 mm on the axis to 5.8 mm on the seventh

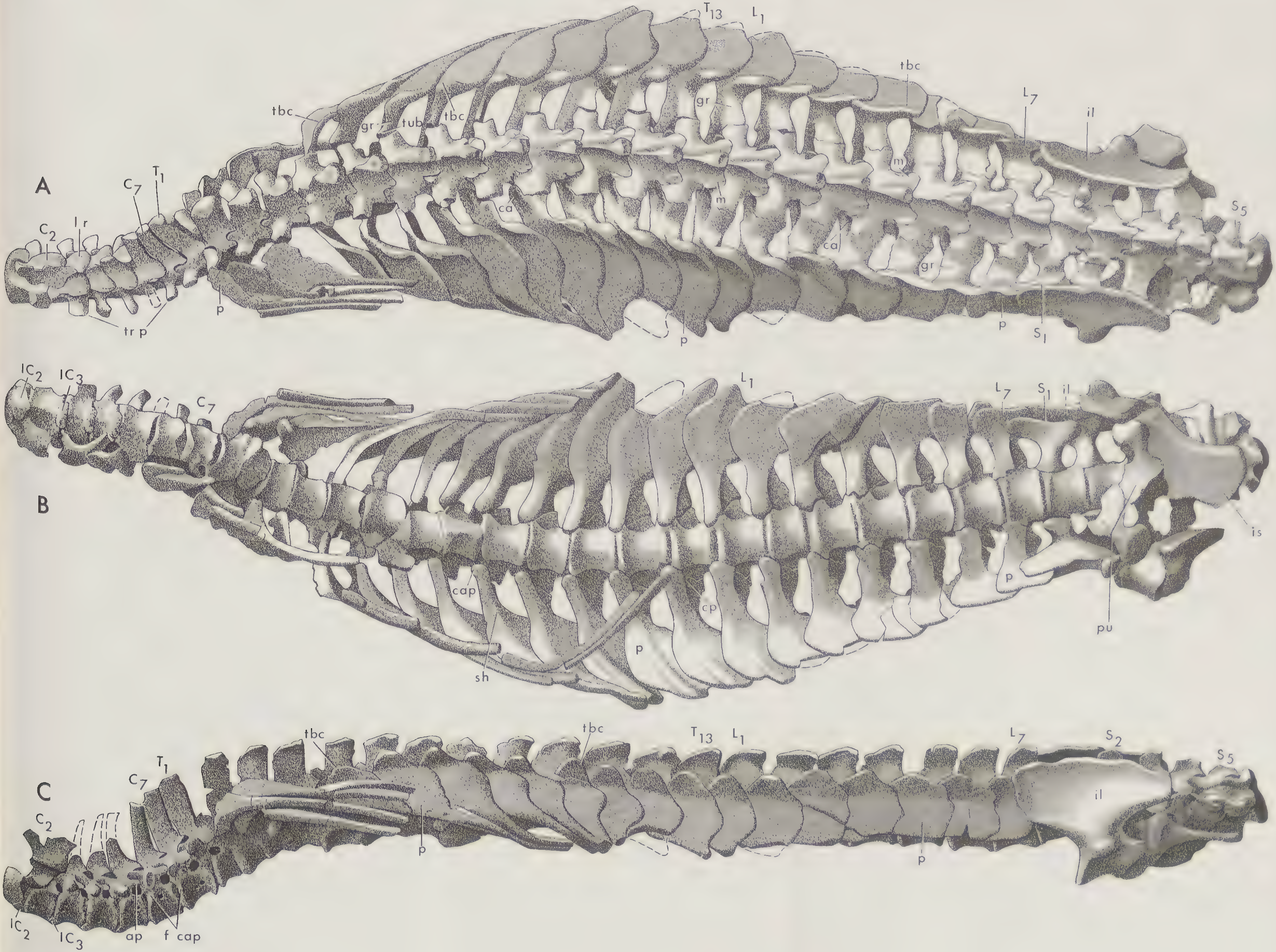
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FIG. 12. The postcranial axial skeleton of *Thrinaxodon* sp., AMMM 5265. A, dorsal; B, ventral; C, lateral views. Dashed lines represent areas reconstructed from other specimens. X1.5. Abbreviations: *ap*, anapophysis; C_1, C_2, etc., first cervical, second cervical, etc.; *ca*, concavity between anterior aspects of capitulum and tuberculum; *cap*, capitulum; *cp*, concavity between posterior aspects of capitulum and tuberculum; *f cap*, facets for capitulum; *gr*, groove between costal tubercle and tuberculum, probably for the ilocostalis muscle; IC_2, IC_3, second and third intercentra; *il*, ilium; *is*, ischium; L_1, L_2, etc., first lumbar, second lumbar, etc.; *l r*, ridge on lamina; *m*, metapophysis; *p*, costal plate; *pu*, pubis; S_1, S_2, etc., first sacral, second sacral, etc.; *sh*, rib shaft; *tbc*, costal tubercle on rib plate; *tr p*, transverse process; *tub*, tuberculum. (see inside)

cervical vertebra, measured between postzygapophyseal extremities. This decrease continues through the fifth cervical, but from the sixth cervical posteriorly there is a gradual increase in this dimension.

A very slight ridge runs anteroposteriorly across the dorsal surface of the laminae of the third through the seventh cervical vertebrae (*l r*, Figs. 3C, 12A). The ridges on the third cervical, barely discernable, bisect each lamina between the base of the spine and the lateral edge of the postzygapophysis. On posterior cervical vertebrae the ridge becomes successively closer to the postzygapophyseal edge because of the narrowing of the laminae and on the seventh cervical it forms the lateral edge of the postzygapophysis. Typically the lateral surface of the pedicles directly ventral to the transverse processes and the ventrolateral sides of the centra are fenestrated by large nutrient canals.

The neural spines are tall, narrow and slightly recurved caudally; the spines on the third through fifth cervical vertebrae show a gradual but distinct anteroposterior tapering toward the apex of the spine (Fig. 12C) that is less developed in the sixth and seventh cervicals. In cross-section cervical spines are elliptical, but on the seventh cervical the posterior margin is swollen in conjunction with the transition to the triangular cross-section found in thoracic spines. The eighth vertebra, i.e., the first thoracic, bears a spine that is distinctly triangular in cross-section and is thus differentiated from all cervical spines.

Thoracic Series

MORPHOLOGY. The morphological transition between the cervical and thoracic series is gradual and not extensive. Intercentra are absent in all postcervical vertebrae, with the possible exception, noted above, of an intercentrum between the seventh cervical and first thoracic vertebrae. Thoracic pleurocentra increase caudally in length and width (Fig. 12B), but this change is slight and they are otherwise morphologically identical to the cervical pleurocentra.

The abrupt change in zygapophyseal orientation is the only definite marker separating thoracic from cervical vertebrae. The facets of the prezygapophyses on the seventh cervical vertebra have an orientation of approximately 55° to the sagittal plane, similar to the facet orientation in the cervical series. On the same vertebra, the articular facets of the postzygapophyses lie within approximately 15° of the sagittal plane, i.e., nearly vertical. The remaining thoracic articulations also appear to be at a similarly high angle, although there is a tendency in the more posterior thoracics to slightly more horizontal orientation, estimated at 20 to 25° from the sagittal plane. A more complete account of the nature of articular facet orientation is given below (see p. 64) for *Galesaurus*. The fact that this specimen of *Thrinaxodon* (AMMM 5265) is articulated prevents more detailed observations.

The increase in length of thoracic vertebrae may be expressed in terms of the distance between the anterior end of the prezygapophysis and the posterior end of the postzygapophysis of a given vertebra. On the first thoracic of AMMM 5265, for example, the length is 7.3 mm; on the sixth, 8.6 mm and on the 13th thoracic, 10.5 mm. Lumbar vertebrae increase only slightly in this dimension.

The transverse processes of anterior thoracic vertebrae do not extend as far laterally as they do in the cervical series. On the fifth cervical vertebra the transverse distance between the lateral margins of the transverse processes is 13.2 mm; on the seventh cervical, where the processes project directly laterad, the distance is 14.0 mm. In contrast, the same measurement on the first thoracic vertebra is 12.9 mm, and on the sixth thoracic it is 11.5 mm. Thereafter, however, the lateral extension of the transverse processes increases; so that at the seventh thoracic vertebra it measures about 12.2 mm (slight damage here introduces uncertainty) and at the 13th and last thoracic vertebra, it is 13.6 mm.

The ribs of the anterior thoracic vertebrae in AMMM 5265 are partially dislodged and the transverse process facets thus exposed show the beginning of a morphological gradient which, in the lumbar series, culminates in confluence of the tubercular and capitular facets. The gradient begins at the first thoracic vertebra, the transverse process of which has a slight anteroventral extension in the direction of the facet for the capitulum. This feature is fully described below, p. 63, from a galesaurid in which all of the thoracic ribs are missing on one side.

The transverse processes also exhibit a progressive displacement throughout the thoracic and into the lumbar series. On the first through the third thoracic vertebrae, the transverse processes arise from the anterior half of the pedicles, and are ventral and slightly posterior to the prezygapophyses. In posterior thoracics the processes become broader anteroposteriorly and at the same time progressively shift posteriorly, i.e., arising from the pedicles at points more nearly equidistant from pre- and postzygapophyses.

The height of the neural spines gradually diminishes from the posterior cervicals, estimated at 9 mm through the seventh thoracic vertebra, approximately 5.5 mm, and thereafter the height decreases only slightly, $<$ 1 mm. From the first through the 13th thoracic vertebrae, the neural spines increase in anteroposterior length, being 3.7 mm on the first thoracic and about 7 mm on the 13th. In cross-section thoracic neural spines are triangular with an expanded, vertical posterior face and two lateral faces converging anteriorly as a thin blade. The anterior margin of the blade, beginning at about the fifth thoracic, is enveloped by a vertical cleft in the posterior margin of the preceding neural spine. Concomitantly the base of the neural spine increases in transverse breadth, particularly across the posterior half of the spinal base. The total increase is on the order of .75 mm and occurs between the first thoracic and the fifth or sixth thoracic vertebrae. Thereafter this dimension remains relatively constant even into the lumbar series. The spinal apices terminate by a rugose tuberosity which bears a shallow depression on the posterior dorsal surface (Fig. 12A). The rim of the depression is defined by a narrow lip of compact bone, but the bottom is floored by spongy bone, often with visible trabeculae. The transition between rim and depression floor is abrupt, as if the compact bone had been removed post-mortem. However the depression is preserved on most vertebrae and in dorsal view shows a distinct morphological gradient from anterior to posterior vertebrae, proving that the feature is not an artifact of preservation. On anterior thoracic vertebrae the lateral edges of the depression are extended and attenuated anteriorly to create a crescent-shaped depression. At approximately the eighth cervical vertebra, the anterolateral edges are reduced and the depression outline assumes an hourglass shape, being somewhat constricted at the

sagittal plane. The depression, identifiable on most thoracic and lumbar vertebrae but absent in the cervical, sacral and caudal series, probably represents the attachment of a supraspinous ligament.

Lumbar Series

MORPHOLOGY. There are seven lumbar vertebrae in *Thrinaxodon.* Lumbar vertebrae differ from thoracic by a slight increase in centrum width, by the development of robust transverse processes, and by the union of parapophysis and diapophysis to form a synapophysis. However the distinction between the lumbar and thoracic series is based on the rib morphology in the posterior dorsal vertebrae. The first lumbar vertebra is designated as the first dorsal vertebra lacking a rib shaft distal to the costal plate of its associated rib. As rib morphology is also gradational, the selection of the first lumbar vertebra is somewhat arbitrary. Nevertheless there is no doubt that the thoracic and lumbar series are sufficiently distinct to warrant separate recognition, despite the fact that they are morphologically intergradational.

The progressive increase posteriorly in centrum width is a continuation of a trend begun in the thoracic series; measured along a transverse line dividing the centrum into equal anterior and posterior halves, the first lumbar centrum is 6.5 mm and the seventh lumbar centrum is 8 mm wide.

The development of more robust transverse processes is also a continuation of a trend begun in the thoracic series. Anteroposteriorly the lumbar processes are broader than in the thoracic series and they are dorsoventrally deeper as well. From the fifth to the seventh lumbar vertebrae the capitular facet (parapophysis) is located on the respective centra only, whereas in the first to fourth lumbar vertebrae the facet is shared by adjacent centra.

The transverse breadth between extremities of the postzygapophyses increases posteriorly, a continuation of the trend begun at the sixth thoracic vertebra; on the first lumbar vertebra in AMMM 5265, for example, the breadth is 7.7 mm, while on the sixth, it is 8.5 mm. An exception is the seventh vertebra which becomes narrower in this dimension, approximately 7.2 mm, in conjunction with the transition to the sacral series.

The length of the anterior lumbar vertebrae, measured between zygapophyses, is 11.1 mm and represents an increase over posterior thoracic vertebrae of about 0.5 mm. The posterior lumbars are equal in this dimension, again with the exception of the seventh lumbar vertebra which, at 9.5 mm, is approximately 1.5 mm shorter than those of the posterior lumbars.

Sacral Series

MORPHOLOGY. The sacral vertebrae are defined on the basis of their rib contact with the medial surface of the iliac blade. The caudal margin of costal plate of the seventh lumbar rib contacts the cranial margin of the iliac blade but in form and func-

tion this vertebra unquestionably belongs to the lumbar series. The sacrum, thus defined, is composed of five vertebrae, not four as claimed by Brink (1954: 119). The specimens available to Brink apparently did not show the fifth sacral rib contact with the ilium, and thus the fifth sacral was mistaken for the first caudal. The posterior margins of the ilium have been lost in AMMM 5265 and therefore it is difficult to be certain about the sacro-caudal division in this specimen. However in two other specimens of *Thrinaxodon* (AMNH 2228, NMB C.143), the sacroiliac articulation is sufficiently preserved to establish definitely five vertebrae in the sacrum. The fifth sacral vertebra lies almost entirely behind the posterior extremity of the iliac blade; the sacroiliac contact is made in this case by a slender, anteroventrally directed process of the fifth sacral rib.

The sacral centra are similar in morphology and dimensions to those of the lumbar series. In AMMM 5265 the distance between the lateral edges of the prezygapophyseal facets of the first sacral vertebra (7.2 mm) is comparable to those of the posterior lumbar series (8.2 mm), but the distance between the lateral edge of the postzygapophyseal facets of the same vertebra is reduced by almost one half (4 mm). On the second sacral vertebra the distance between the lateral edges of the postzygapophyses decreases to 3.7 mm, but thereafter successively increases on the third through fifth sacral vertebrae; on the last it measures 5.3 mm. The zygapophyseal facets articulate at extremely high angles, i.e., nearly parallel to the parasagittal plane, and the zygapophyses are much smaller than lumbar zygapophyses. There are anapophyses, as in the lumbar series, but they are smaller.

The short, stout transverse processes of the first sacral vertebra are less robust but otherwise very similar to those of the seventh lumbar. Sacral transverse processes posterior to the first sacral vertebra are successively more slender.

The sacral neural spines are less elongate anteroposteriorly than those of the lumbar series and their apices lack the tuberosities and depressions characteristic of the dorsal vertebrae. The spines of the fourth and fifth sacral vertebrae are essentially like those of the caudal series, being short and having a more or less oval apex.

Caudal Series

MORPHOLOGY. Broom (1932b: fig. 41) gave a reconstruction of *Thrinaxodon liorhinus* with 16 caudal vertebrae, assuming a sacral count of four. Broom made no mention of how he determined this number nor did he describe the specimen on which he based his reconstruction. Describing cynodonts in general, Broom (1932b: 263) wrote that there were "a small number of caudals perhaps twelve to twenty." Brink (1954: 119, fig. 2) followed Broom, illustrating 16 caudal vertebrae. But Brink believed the sacrum contained only four vertebrae, whereas it has been shown (see foregoing section on sacral vertebrae) that Brink's first caudal contacts the ilium and is actually the fifth sacral. Hence in Broom's and Brink's reconstructions there are 15 caudal vertebrae, not 16.

The actual number of caudal vertebrae in *Thrinaxodon*—or in any cynodont—is in doubt because available specimens are incomplete. In NMB C.392 there are only five and one-half caudals and in NMB C.142 there are three; both specimens are in-

completely prepared and in damaged condition. In AMNH 2228, four caudal vertebrae and part of the fifth are preserved and have been acid prepared. This last specimen is the only material from which an accurate description of cynodont caudal morphology can be made.

In AMNH 2228 the neural spines decrease in height from the first caudal (4 mm) to the third caudal vertebra (2.5 mm). The neural spine of the fourth caudal is missing. The spines are less elongate anteroposteriorly than in the sacral series, and their apices are oval.

The zygapophyseal articulations between the fifth sacral and first caudal and between the first two caudal vertebrae appear to be nearly vertical in dorsal view, much as in the sacral series. The articulations between the second and third and between the third and fourth caudal vertebrae are more oblique but are within 20° of the parasagittal plane. However the third and fourth caudals have been partially disarticulated and show that the nearly vertical facet of each prezygapophysis turns medially and horizontally at the base of the prezygapophysis. Thus each prezygapophysis is half of a cup-shaped depression. Postzygapophyses likewise bear a vertical facet area laterally and a horizontal facet area medially. This feature will be described in more detail below with reference to thoracic vertebrae in *Galesaurus*.

Anapophyses are present, but are much smaller than in the sacral or pre-sacral series.

Transverse processes are robust and very short. They are directed posterolaterally and ventrally, whereas sacral transverse processes are directed more or less laterally. Since a separate capitulum is not developed on caudal ribs, the transverse process is the sole structure joining caudal ribs and vertebrae. In AMNH 2228 the transverse process-rib articulation appears to have been at least partly ossified.

It is possible that there were less than 15 or 16 caudal vertebrae in *Thrinaxodon* judging by the rapid diminution of vertebra size. The length of the second caudal in AMNH 2228 is 5 mm, while the fifth caudals is 4 mm, compared to a length of 7.3 mm at the first lumbar. On the basis of available material, I would estimate a caudal count of 10 to 15.

Broom (1932b: fig. 92) and later Brink (1954: fig. 2) reconstructed *Thirnaxodon* as having chevron bones, or haemapophyses, associated with most of the caudal vertebrae. There is no substantial evidence of these in AMNH 2228 other than a few unidentifiable bone scraps which are probably broken pieces of ribs or vertebrae. There is thus considerable doubt that *Thrinaxodon* possessed caudal chevrons.

Ribs

Ribs are associated with all cervical, thoracic, lumbar and sacral vertebrae. All caudal vertebrae, insofar as known, also possess ribs.

Cervical Ribs

MORPHOLOGY. In AMMM 5265, the proximal ends of several cervical ribs are preserved on the right side. Their damaged condition limits description to the following

observations. In lateral view a typical proximal rib end is a small, triangular plate; the apex of the triangle is continuous with the (broken off) rib shaft, while the base lies against the vertebra. This triangular expansion for the most part represents the diverging capitulum and tuberculum, which are not separated as distinct processes. The dorsal margin of this triangular expansion bears a narrow, vertical flange which represents a small cervical costal plate. Cervical ribs were probably directed posterolaterally as well as ventrally. There could have been little, if any, overlap between the platelike proximal ends of adjacent ribs because they were probably oriented more or less vertically. Nothing can be described of the shape and orientation of the capituli and tuberculi nor of the length of cervical ribs.

Thoracic Ribs

MORPHOLOGY. No sharp morphological discontinuity occurs between the cervical and thoracic ribs, although the two rib types in the middle of each series are well differentiated. The ribs of the sixth cervical to third thoracic vertebrae are of intermediate morphology.

The capitulum of thoracic ribs is a stout process which, like that of the cervical ribs, is continuous with the distal shaft of the rib by a ridge along the ventral aspect of the costal plate (*cap*, *sh*, Fig. 12B). The capitulum and tuberculum (*tub*, Fig. 12A) of the anterior thoracic ribs lie relatively close together; the capitulum is ventral and slightly anterior to the tuberculum and directed medioventrally and slightly anteriorly. This condition approximates that found in the cervical series. In the posterior thoracics beginning at the seventh or eighth thoracic, the capitulum progressively shifts its orientation anteriorly so that the angle formed between the posterior edge of the capitular process and the vertebral column decreases from approximately 85° at the fifth thoracic to 70° at the tenth thoracic (Fig. 12B). Thereafter the trend is reversed and the capituli become directed more medially and less anteriorly; at the first lumbar the capitular process forms a 90° angle with the vertebral column.

In the posterior thoracics the capitulum becomes progressively more elongate until, at the 13th thoracic, it extends almost to the level of the ventral surfaces of the centra. The capitulum also becomes increasingly robust, a trend which culminates in the confluence of capituli and tuberculi in the lumbar ribs. Thoracic ribs are not fused to the transverse processes as are the lumbar ribs, although the ribs of the 12th and 13th thoracic vertebrae appear to have a serrate suture and the joint may have had reduced mobility.

The tuberculi of thoracic ribs are short, stout processes, each separated from the associated capitulum ventrally by a thin lamina of bone. As stated previously, the tuberculi of the anterior thoracics lie above and slightly behind the capituli, and therefore the bony laminae between them are oriented almost vertically. In the posterior thoracics the transverse processes broaden anteroposteriorly and the tuberculi likewise broaden.

In the anterior thoracics the anterior surfaces of the laminae between capituli and tuberculi are flat. Posterior to the seventh thoracic rib these surfaces become succes-

sively more concave. Concomitantly an anteriorly reflected lip develops on the anterior margin of each capitular process, and consequently the area between each capitulum and tuberculum becomes a broad concavity (*ca*, Fig. 12A). The opposite, posterior surfaces of the laminae on anterior thoracic ribs are similarly flat, but become progressively modified into a deep concavity by the anteroposterior lengthening of the capituli and tuberculi and by the posterior migration of the former (*cp*, Fig. 12B). Facing pairs of concavities, one anterodorsal, another posteroventral, thus form a wide sinus adjacent to each intervertebral foramen in the posterior thoracic and lumbar series.

The most bizarre feature of the presacral ribs in *Thrinaxodon* and in many other cynodonts is the localized expansion of each shaft, conveniently referred to as a costal plate (*p*, Fig. 12). No single description of a cynodont costal plate would suffice because costal plates are structurally very different not only with respect to vertebral regions, but also among cynodont families. A description of the costal plates in *Thrinaxodon* may conveniently begin with those on the anterior thoracic ribs; the cervical costal plates were probably similar to the anterior thoracics, but, as indicated in the preceding section, are known only from poorly preserved material. The dorsal edge of the tubercular process is thin and blade-like in the anterior thoracic ribs and is confluent laterally with the rising dorsal margin of the costal plate (Fig. 12A). At the fourth or fifth thoracic rib, however, the costal plates of the ribs become differentiated from the dorsal edge of the capitular process by an incipient costal tubercle (*tbc*, Fig. 12A, C) which becomes progressively larger in the remaining thoracic and lumbar series. Typically developed from the sixth thoracic rib posteriorly, the costal tubercle is a bulbous swelling on the dorsomedial edge of the costal plate. Between the costal tubercle and the transverse process the dorsal edge of all thoracic capitular processes posterior to the sixth thoracic rib becomes anteroposteriorly broader as well as transversely wider. Beginning with the fifth or sixth thoracic rib each of these broad dorsal edges is grooved anteroposteriorly (*gr*, Fig. 12A), creating the impression of a paraxial sulcus which extends to the sacrum but which is partitioned transversely by the intercostal spaces.

The costal plates of the thoracic ribs display a complex morphological gradient which is partly obscured by their imbricating relationship. In all thoracic ribs except the 13th the shaft is continuous between the capitulum and the distal costal shaft by means of a distinct ridge across the ventral side of the costal plate (*cap*, *sh*, Fig. 12B). On the 13th thoracic and first lumbar this ridge is discontinuous and on all the following lumbar ribs it is lost. The costal plate of an anterior thoracic rib is basically a vertical, supracostal flange arising from the dorsal aspect of the rib shaft; only a small part of the plate extends ventrally below the rib shaft. The external surface of an anterior thoracic plate faces anterolaterally and is shallowly concave by virtue of the lateral reflection of the incipient costal tubercle above and the ventral edge of the plate below.

The costal plates of the middle and posterior thoracic ribs progressively undergo the following changes. The costal tubercle differentiates as a bulbous, ventral reflection of the otherwise nearly horizontal costal plate; the remainder of costal plate faces dorsally and slightly anterolaterally. The posterior half of the costal plate expands and lies on the anterior half of the next posterior plate, resulting in extensive imbrication of adjacent plates. The posterior edges of the fifth through tenth thoracic costal are

swollen and in effect form a second costal tubercle, a feature absent on all remaining thoracic and lumbar ribs.

The costal tubercles of thoracic ribs are aligned parasagittally with those of the lumbar ribs which in turn are aligned with the iliac blade (Fig. 12A). Thus the axial skeleton shows a major subdivision along the line of the costal tubercles: the costal plates and shafts lie laterally, and a broad channel lies medially between the tubercles, or iliac blade, and the neural spines. The width of the channel, measured from the apex of the costal tubercle to the sagittal plane, is greatest at the level of the twelfth and thirteenth thoracic vertebrae (13.1 mm in AMMM 5265) and is only slightly less at the fifth thoracic (11.4 mm) and at the seventh lumbar (11.9 mm). Anterior to the fifth thoracic rib the channel is difficult to define because of the rib reorientation and diminution of the costal tubercles.

The largest costal plates in terms of area are estimated to be those of the eleventh to thirteenth thoracic ribs. Accurate measurement of the relative sizes of costal plates requires a disarticulated skeleton.

Little can be described of the rib shafts which extend beyond the costal plates because they are very slender and commonly are either lost or damaged. In anterior thoracic ribs the shaft comprises about three-quarters of the rib length. On the seventh and eighth thoracic ribs the shaft is estimated to have been a little over half the rib length. On the 10th thoracic the shaft is considerably shortened and on the 13th it is a mere spike. Each of the first three lumbar ribs bears a tubercle; the tubercles successively decrease in size from first to third. No vestige of a rib shaft can be detected on the fourth through seventh lumbar ribs.

Thoracic rib shafts preserved with USNM 22812 are extremely compressed in cross-section. The posterior aspect of the shaft, as it emerges from under the costal plate, bears a deep, longitudinal groove. As the groove runs along the shaft, it comes to lie more on the dorsal aspect of the shaft. The groove, which cannot be traced to its terminus because no thoracic rib is sufficiently complete, probably represents an intercostal neurovascular sulcus.

Lumbar Ribs

MORPHOLOGY. Lumbar ribs are synostosed to the transverse processes along a serrate suture and the articulation is not "loose" as suggested by Brink (1958: 21). The capitular processes become progressively shorter toward the sacrum and shift dorsally to closer proximity with the tuberculi. Therefore lumbar capitular processes reverse the trend of the thoracic series in which the capituli become progressively longer and move lower on the centrum rim. Lumbar capitular articulations also shift posteriorly until, at the sixth lumbar, the capitulum contacts only the centrum of the sixth lumbar and the articulation is no longer intervertebral. The tuberculi of all lumbar ribs are broad. With the possible exception of the first two or three lumbar ribs, it appears that lumbar capitular and tubercular facets are essentially confluent and thus fuse with a synapophysis.

The costal plates of the lumbar ribs are gradually transformed from the lanceolate shape of the thoracic plates to a subrectangular outline (Fig. 12C). In the lumbars the

costal tubercle becomes anteroposteriorly longer and narrower (Fig. 12A). The plates continue to imbricate so that the long, narrow costal tuberosities form an undulating ridge of bone which is aligned parasagittally with the iliac blade. The ventral parts of the costal plates are reduced in size relative to the analogous area on thoracic costal plates; furthermore, they are gradually reoriented to face more laterally and less dorsally.

The anterior margins of lumbar costal plates are concave and do not extend significantly forward of the conjoined capitular and tubercular processes. Such a construction permits the convex medial surface of one costal plate to project posteriorly over the concave lateral surface of the next (posterior) costal plate (Fig. 12C).

As a series the lumbar plates become progressively smaller toward the ilium. The height of the seventh lumbar costal plate equals that of the adjoining ilium and the dorsal and ventral edges of the costal plate and iliac blade are continuous. In AMMM 5265, Fig. 12C, both ilia have been displaced dorsally post-mortem. Furthermore the posterior margin of the seventh lumbar costal plate contacts the anterior margin of the iliac blade, making the lateral surfaces of the ilium and lumbar plates continuous.

Sacral Ribs

MORPHOLOGY. All five sacral ribs are fused to synapophyses. Not only are the capitular and tubercular facets confluent, as they are on lumbar ribs, but the capitular and tubercular processes also fuse and cannot be distinguished. In the lumbar ribs the processes are closely conjoined but can be morphologically delineated. The first sacral rib is the largest. Its costal plate, which is as long but not as high as that of the seventh lumbar, bifurcates anteriorly. The dorsal and ventral parts of this bifurcation clasp the medial side of the seventh lumbar costal plate. The ventral part, which is the larger of the two parts, extends anteriorly to overlap on the lower medial surface of the seventh lumbar costal plate (*S1*, Fig. 12B); the smaller dorsal part similarly overlaps the upper medial surface (*S1*, Fig. 12A, left side). The remainder of the first sacral rib plate, posterior to the bifurcation, contacts the medial surface of the ilium, thus forming a bond between the seventh lumbar costal plate and the pelvis. The second through the fourth sacral ribs progressively diminish in size and do not bear costal plates, although the second and third sacral ribs are slightly expanded at their iliac contact. All sacral ribs are directed laterally and, with the exception of the fifth sacral, their distal ends are flattened dorsoventrally and elongated anteroposteriorly. The fifth sacral rib is approximately triangular in shape (Fig. 12A, left side). The apex of the triangle contacts the transverse process. The anterior corner of the triangle is a slender rod which passes anterolaterally to contact the posterior, medial extremity of the ilium (see AMNH 2228). The posterior corner of the triangular rib passes posterolaterally to make contact with the first caudal rib. The nature of this contact is not sufficiently preserved in any specimen to permit description.

The sacroiliac joint is not synostosed and probably represents a synchondrosis. In most specimens (including AMMM 5265) the ilia are either displaced or are altogether disarticulated from the sacral ribs.

Caudal Ribs

MORPHOLOGY. Ribs are preserved with the first four caudal vertebrae of AMNH 2228. The capitulum and tuberculum are fused and cannot be distinguished. Each shaft is swollen at the contact with the transverse process, is constricted about the middle, and expands anteroposteriorly at the lateral terminus. The lateral terminus is dorsoventrally flattened. It is probable that the first and second and second and third ribs made contact by virtue of their lateral expansion, but the nature of this contact is not clear. The fourth caudal rib is dumbbell-shaped and much smaller than the others. All caudal ribs are directed posterolaterally and somewhat ventrally.

4. THE POSTCRANIAL AXIAL SKELETON OF OTHER GALESAURIDS

MATERIAL. Parrington (1934) described the vertebral column and rib morphology of *Galesaurus* from three specimens collected in the *Lystrosaurus* zone near Harrismith. Two of the specimens, one an isolated and incomplete lumbosacral series with the third lumbar through second sacral vertebrae (UMC R.2733), the other an almost complete vertebral column with the second through fourth sacral vertebrae (UMC R.2722), are not associated with any diagnostic cranial remains. Generic identification was founded primarily on the presence of anapophyses (Parrington, pers. comm.) which are also present in the third specimen consisting of a *Galesaurus* skull and the first four cervical vertebrae (UMC R.2721). Anapophyses are common to the vertebrae of most cynodonts, however, and the generic assignment of the first two specimens is in doubt. Nevertheless the vertebrae are unquestionably galesaurid and are, in fact, indistinguishable from *Thrinaxodon* itself. Since this generically unidentifiable material reveals certain features not clearly seen in other galesaurid specimens, it will be accorded further description. In addition the cervical vertebrae of Parrington's third specimen, which is assuredly *Galesaurus*, and six thoracic vertebrae and ribs of another positively identified *Galesaurus* (SAM K.1119) will be described. They, too, are indistinguishable from *Thrinaxodon* material and provide a clearer understanding of the galesaurid axial morphology.

Cervical Series

MORPHOLOGY. The third through seventh cervical vertebrae are indistinguishable from those of *Thrinaxodon.* The neural spines of the third, fourth and fifth cervicals are fusiform in cross-section, taper towards the apex, and are recurved posteriorly. The spine of the third cervical is the most sharply recurved to permit space for the posteriorly projecting axis blade. The anteroposterior ridge across the dorsal laminar surface appears to be relatively higher, although in this specimen the lateral edges of the zygapophyses are missing. The angles of zygapophyseal articulations and the morphology and orientation of the robust transverse processes are the same as in *Thrinaxodon.* Parrington (1934: 49) claimed that the zygapophyseal articulation between the third and fourth cervical is "rather more horizontal" than that between the axis and the

third cervical. In fact the reverse is true; as in *Thrinaxodon*, the articulation of the zygapophyseal facets of the axis and third cervical makes an angle of approximately 45° with the horizontal and between the third and seventh cervical vertebrae the angle increases to about 55°. On UMC R.2722 the articulations show the same features, although they are somewhat obscured by breakage.

Thoracic Series

MORPHOLOGY. In the 13 thoracic vertebrae of UMC R.2722 no substantial differences from *Thrinaxodon* are apparent although the specimen is only partially prepared and somewhat damaged. The morphological gradient of facets for the tuberculum is evident. In the anterior thoracic vertebrae the capitular fovea is composed of two separate demifacets borne on the adjacent rims of successive vertebrae. These demifacets, located on the dorsolateral aspect of the rim below the pedicle-centrum suture, together form a wedge-shaped fovea. The caudal demifacet is partially formed on the base of the pedicle projecting anteriorly beyond the rim of the centrum. Toward the posterior thoracic vertebrae, the fovea progressively increases in size and shifts its position caudally, i.e., by increasing the demifacet size of the caudal half and decreasing the demifacet size of the cranial half.

In the most anterior thoracics the transverse process is crescentic in cross-section (*tr p*, Fig. 13A). An anteroventral extension of the process almost reaches the pedicle-

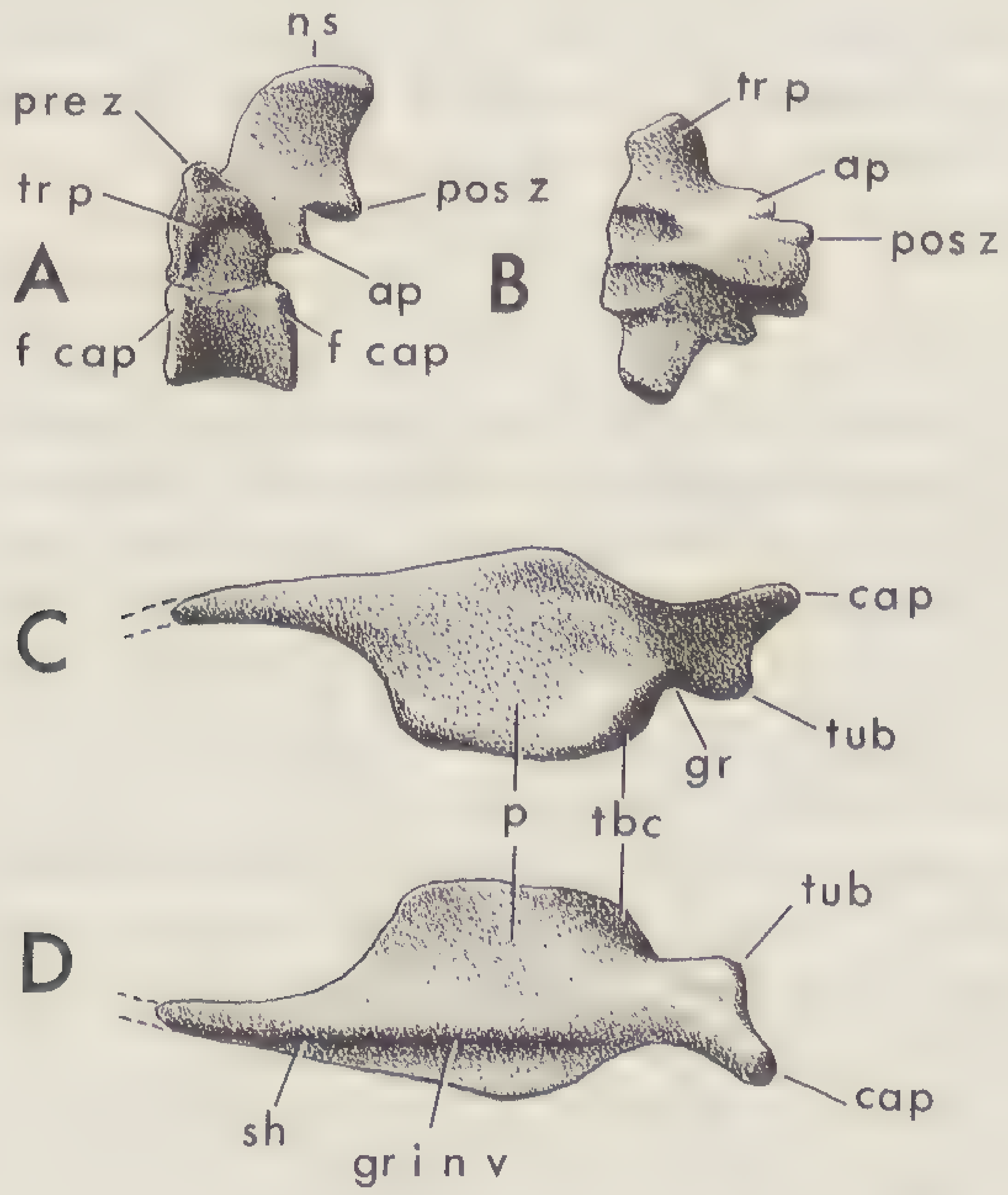

FIG. 13. *Galesaurus planiceps*, SAM K. 1119. A, lateral; B, dorsal views of first or possibly second thoracic vertebra. C, dorsal; D, ventral views of fifth or possibly sixth thoracic rib. Approx. X1.5. Abbreviations as in FIG. 12 except: *gr i n v*, groove for intercostal nerve and vessels; *n s*, neural spine; *pos z*, postzygapophysis; *pre z*, prezygapophysis.

centrum suture, while a posteroventral extension reaches the base of the anapophysis. For the most part the facet for the tuberculum faces laterally. In the more posterior thoracics the facet becomes less crescentic and more fusiform in cross-section as the size of the cranial capitular demifacet increases and as the facets for the capitulum and tuberculum nearly merge. In the lumbar vertebrae both facets are confluent.

An acid-prepared specimen of *Galesaurus* (SAM K.1119) preserves a series of six thoracic vertebrae which are completely freed of matrix and on which further and more detailed observations can be made than is possible on the Cambridge specimens. The vertebrae are distinguished from the cervical series by their relatively low, anteroposteriorly wide neural spines, and from the lumbar series by the character of their associated ribs (see below, p. 66). The vertebrae, which are hereafter referred to numerically, 1—6, are tentatively identified as being the first through the sixth thoracic vertebrae, or possibly the second through seventh. This identification is made possible by certain morphological changes which are comparable to those in the anterior thoracics of *Thrinaxodon* (AMMM 5265) and *Galesaurus* (UMC R.2722). The height of the neural spines, measured from the apices to a horizontal line tangential to the dorsal rim of the prezygapophyses, decreases from 7 mm at 1 to 4 mm at 6. Neural spines of posterior thoracic vertebrae in *Thrinaxodon* do not show this degree of differentiation (see p. 54). The six vertebrae also show an increase in the transverse breadth of the neural spine base, as in the anterior thoracics of *Thrinaxodon* (AMMM 5265).

The demifacets for the capitulum are poorly preserved in SAM K.1119 and are restored in the vertebra illustrated (*f cap*, Fig. 13A). The loss of this feature is partly the result of acid preparation which separated the vertebra along the pedicle-centrum suture; this region was apparently incompletely ossified. The morphology of the transverse process and its facet for the tuberculum is clearly shown, however, and is identical to those on the anterior thoracic vertebrae of UMC R.2722.

The zygapophyses are well preserved and permit detailed description of features obscured in other articulated specimens. The articular facets of the prezygapophyses are rounded, cuplike depressions which are open dorsally and anteriorly (Fig. 13B). If flattened out, the facet would be oval in outline with the long axis transverse to the vertebral axis. The prezygapophyses are not the typical protruding processes or "stalks", for part of the articular facets are actually recessed within the laminae. Each facet is composed basically of a nearly vertical wall laterally and a nearly horizontal floor medially. The two horizontal sectors are separated medially by a ridge which is an anterior continuation of the neural spine.

The postzygapophyses are distinct processes protruding posteriorly from the base of the neural spine (*pos z*, Fig. 13A, B) and are separated by a groove which receives the basal part of the spine of the succeeding vertebra. They extend beyond the rim of the centrum in order to couple with the prezygapophyses recessed in the laminae of the succeeding vertebra. A posterior articular facet is divisible into lateral and ventral surfaces, corresponding in orientation to the lateral wall and medial floor of the prezygapophyses. In previous discussion of the angle of interzygapophyseal articulation in *Thrinaxodon*, only the orientation of the lateral aspect of the facet could be estimated because the medial (horizontal) part of the facet was obscured by the articulation. The six vertebrae of *Galesaurus* show that the orientation of the lateral (vertical) as-

pect of the zygapophyseal facets is progressively modified in the anterior thoracic series, as in *Thrinaxodon*, although the medial (horizontal) aspect, obscured in the AMMM 5265 *Thrinaxodon*, persists unchanged. The exact degree of facet reorientation is difficult to determine because the delicate facets have been somewhat deformed plastically. The orientation of facets relative to the sagittal plane was estimated by protractor from photographs taken of each vertebra in anteroposterior view. The lateral aspect of the prezygapophysis of the first vertebra is estimated to be 10° (±5°) to the sagittal plane, while that of the postzygapophysis of the same vertebra is 14° (±5°). Using the same technique the lateral prezygapophyseal aspect of the sixth vertebra is approximately 25° (±5°) and that of the postzygapophysis is 33° (±5°). Despite the uncertainties engendered by plastic deformation, the zygapophyseal reorientation toward a more horizontal plane is definitely demonstrated.

An increase in the length of the laminae, measured anteroposteriorly between the tips of the zygapophyses, characterizes these vertebrae as it does the thoracics of *Thrinaxodon*. On the first vertebra the length is 9 mm and it increases at each successive vertebra to 10.2 mm on the sixth.

As in the anterior thoracics of *Thrinaxodon* the transverse processes of the six vertebrae are directed laterally and slightly anteriorly and progressively increase in anteroposterior breadth, viewed from above. The degree of cranial inclination is greater at the first vertebra than at the sixth. These vertebrae also show the same progressive modification of the tubercular facet seen in *Galesaurus* (UMC R.2722) and *Thrinaxodon*. The incipient anteroventral extension of the transverse process on the first vertebra (*tr p*, Fig. 13A) increases in thickness and extent so that at the sixth vertebra the facets for the capitulum and tuberculum are nearly confluent.

Lumbar Series

MORPHOLOGY. The lumbar series of UMC R.2722 is probably composed of seven vertebrae as in *Thrinaxodon*, but it is impossible to verify the count because the lumbar ribs are poorly preserved and the lumbosacral articulation is not exposed. Parrington (1934: 51) believed the 28th vertebra to be a lumbar, which would give a total count of eight lumbar vertebrae, assuming that there were 13 thoracics as in *Thrinaxodon*. However, the prezygapophyseal articulation of the 28th vertebra is sufficiently preserved on the left side to show that the interzygapophyseal breadth is reduced relative to that of the 27th vertebra, i.e., the seventh lumbar vertebra. This same feature is characteristic of the interzygapophyseal articulation between the seventh lumbar and first sacral in *Thrinaxodon* and on this basis the 28th vertebra would appear to be the first sacral—not a lumbar as suggested by Parrington. The cranial edge of the iliac blade is broken off in this specimen but if reconstructed would overlap the transverse process of the vertebra in question and thus substantiate its sacral position. Therefore the presacral vertebral count in *Galesaurus* is probably the same as in *Thrinaxodon*, i.e., seven cervicals, thirteen thoracics, and seven lumbars; furthermore, the morphology of the vertebrae cannot be shown to be recognizably different on the basis of UMC R.2722 and SAM K.1119.

Sacral Series

MORPHOLOGY. The sacrum of UMC R.2722 is so poorly preserved and incompletely prepared that little can be added to Parrington's description. As in the sacrum of *Thrinaxodon* the neural spines are more slender than those of the lumbar series and the zygapophyseal articulations are nearly vertical. The iliac blade extends sufficiently posteriorly to have included a fifth sacral vertebra which would be numbered 32 in the complete vertebral column. Unfortunately the posterior half as well as the transverse processes of this vertebra have been broken away, but the mere length of the iliac blade is evidence that the sacrum includes five vertebrae as in *Thrinaxodon.*

Ribs

MORPHOLOGY. The only ribs positively associated with *Galesaurus* (SAM K.1119) are from the thoracic region. These ribs are best preserved on the left side and belong to the middle four of six vertebrae, which are all that remain of the vertebral column. The vertebrae with which they are associated are either the second through fifth or third through sixth thoracic (see above, p. 64). In no way can these ribs be shown to differ from comparable anterior thoracic ribs of *Thrinaxodon.* However, since these ribs display several features more clearly than in any specimen of *Thrinaxodon,* and because they have been acid-prepared and disarticulated, further description of these aspects is warranted.

The articular facets of the capitulum and tuberculum are well preserved on the fourth rib, i.e., the fifth or sixth thoracic (Fig. 13C, D). The capitular facet is small, circular and slightly convex; it obliquely truncates the terminus of the capitular process. The tubercular facet is straight and narrow, extending from the tubercular process along the capitular process almost to the capitular facet. It is slightly narrower than the capitular facet. The dorsal third of the facet faces medially, the central third posteromedially and the ventral third medially again. The ventral third sharply attenuates and does not reach the end of the capitular process. The dorsal half of the facet is flat but the ventral half is slightly concave. The orientation and the surface relief of both facets probably vary with ossification or position and these features should not be regarded as constant. For example, the 11th (or possibly the 12th) thoracic rib associated with ?*Galesaurus* (UMC R.2722) has a capitular facet which is round and bulbous and a tubercular facet which is concave along its entire length and faces medially with no posterior twisting of the center section.

In *Thrinaxodon* the thoracic ribs posterior to the fifth, as well as all lumbar and sacral ribs, show a distinct anteroposterior groove across the dorsal edge of the tubercular process (*gr,* Fig. 12A; see p. 59). This groove is incipiently developed in the anterior thoracic ribs, but becomes progressively wider and longer with the successive increase in size of the thoracic and lumbar tubercular processes. The preservation of the first four thoracic ribs in *Thrinaxodon* (AMMM 5265) does not reveal the details of

this region. On *Galesaurus* (SAM K.1119), however, the morphology is clear. On the rib of vertebra five, i.e., either the fifth or sixth thoracic, the edge is rather narrow but the groove is incipiently developed (*gr*, Fig. 13C). The analogous area on ribs of vertebrae two, three and four is exceedingly blade-like and straight and all traces of the groove between the tuberculum and costal tubercle are lost.

The imbrication of the costal plates in *Thrinaxodon* (AMMM 5265) obscures certain details that are evident in the disarticulated ribs of *Galesaurus* (SAM K.1119). The anterior margin of the plate is slightly convex and reflected dorsally (Fig. 13C). As the posterior margin is also reflected dorsally especially near the costal tubercle, the entire dorsal surface is gently concave. A shallow groove adjacent and parallel to the anterior margin receives the posterior ventral surface of the preceding costal plate. A deep groove, perhaps representing the course of an intercostal nerve and vessels, typically occurs on the ventral surface of a plate between its anterior lip and the shaft (*gr i n v*, Fig. 13D). This groove continues distally on the shaft beyond the terminus of the costal plate, and gradually fades out 1 cm from the costal plate. As it fades out it shifts its position toward the dorsal aspect of the shaft.

5. THE POSTCRANIAL AXIAL SKELETON OF *CYNOGNATHUS*

MATERIAL. *Cynognathus crateronotus* was described and figured by Seeley (1895b) from an incomplete and crudely prepared skeleton of a single individual (BMNH R.2571). The axial skeleton is relatively complete, although the posterior caudal vertebrae are missing as are most of the cervical and thoracic ribs. There has never been any further detailed investigation into the axial morphology of this well-known cynodont genus, primarily for lack of new material. In addition to the type material very fragmentary remains are known from two collections (BPI 1675; NMB C.2710 and NMB C.2713) in which disarticulated remains of many individuals of this genus and *Diademodon* are preserved together. In addition there is an incomplete and somewhat crushed skeleton of a single individual of *Cynognathus* sp. (UCMP 42729). Broili and Schröder (1936) have described the axis and several cervical vertebrae from a large cynodont believed to be *Cynognathus*. All of the above material, even if considered together, does not permit a complete evaluation of the *Cynognathus* axial skeleton. Nevertheless certain differences as well as similarities to other cynodonts are worth describing.

Cervical Series

MORPHOLOGY. The atlas-axis complex, insofar as known, is basically similar to that in other cynodonts. The primary differences are the rather rectangular outline of the first intercentrum and the more ventral orientation of the intercentral facet on the atlas centrum.

The number of cervical vertebrae in *C. crateronotus* (BMNH R.2571) is seven, not six as suggested by Seeley (1895b: 97). The division between cervical and thoracic vertebrae is based on the same criteria as in *Thrinaxodon*. First, the prezygapophyses of the seventh cervical and the zygapophyses of all vertebrae anterior to this vertebra are inclined at an angle of about 45°. The postzygapophyses of the seventh cervical and the zygapophyses of the anterior thoracic vertebrae are nearly vertically inclined. Second, the transverse processes of the first six cervical vertebrae are directed posterolaterally and ventrally; the transverse processes of the seventh are approximately at the same level as are those anterior to it, contrary to Seeley's claim, but they are directed laterally only. The transverse process of thoracic vertebrae are directed more or less anterolaterally as in *Thrinaxodon*.

The cervical vertebrae of *Cynognathus crateronotus* (BMNH R.2571) are similar to those of *Thrinaxodon* in a number of features. The neural spines are fusiform in cross-section and are slightly recurved caudally. The spine of the seventh cervical vertebra, although broken off near the base, appears to have been intermediate in cross-section between the slender cervical spines and the wider, more robust thoracic spines. The width between zygapophyses is greatest at the cranial end of the cervical series and continues to diminish throughout the anterior thoracic series as in *Thrinaxodon*. Intercentra are associated with the first six vertebrae and possibly with the seventh as well; the interspace of the sixth and seventh cervical vertebrae is obscured by a displaced rib. As in *Thrinaxodon* the ventral aspect of the cervical centra bears a longitudinal keel along the midline. The keel is most prominent on the axis and diminishes in size on succeeding centra until on the first and second thoracic vertebrae it is merely a swelling. Anapophyses are absent in *Cynognathus* cervical vertebrae (see Broili and Schröder, 1936: 66).

Thoracic Series

MORPHOLOGY. There are 15 thoracic vertebrae in *Cynognathus crateronotus* (BMNH R.2571), two more than in *Thrinaxodon*. The first lumbar is distinguished from the 15th and last thoracic by the character of its associated rib (discussed below); otherwise, there is no sharp morphological discontinuity between thoracic and lumbar vertebrae. Insofar as may be determined from the partially prepared type material, the thoracic vertebrae are morphologically similar to those of *Thrinaxodon*. A gradual and very slight increase in the length of centra is evident. The total increase is approximately 3 mm from the anterior thoracics, which measure 29 mm, to the posterior thoracics, which measure ahout 32 mm.

The zygapophyseal facets of the anterior thoracics are inclined nearly vertically. This condition prevails throughout most of the thoracic series, but in the 13th through 15th thoracics, and in the lumbar series as well, there appears to be a shift towards a more horizontal orientation. The incompleteness of preparation, however, does not permit verification of this reorientation, which is positively known in *Thrinaxodon*.

The neural spines of the thoracic vertebrae are shorter than those of the cervicals; they differ from the thoracic spines of *Thrinaxodon* in being less triangular and more fusiform in cross-section.

Another difference is in contour of the dorsal surface of the transverse processes. In *Thrinaxodon* the dorsal surface of all thoracic transverse processes are essentially cylindric, being smoothly convex from front to back. In *Cynognathus* the dorsal surface of the first through tenth thoracic transverse processes are convex anteriorly, similar to those in *Thrinaxodon*, but posteriorly there is a transverse groove not represented in *Thrinaxodon*. The remaining transverse processes are as in *Thrinaxodon*.

Lumbar Series

MORPHOLOGY. There are seven lumbar vertebrae as in *Thrinaxodon*. The length of each lumbar centrum in BMNH R.2751 is the same as that of a posterior thoracic centrum. There is a gradual and slight increase in the width of lumbar centra from 25 mm at the second lumbar to 28 mm at the seventh. The transverse width between prezygapophyses continues to increase, as in the thoracic series; on the first lumbar the width is 23 mm, while on the seventh it is 25 mm. Conversely the transverse width between the tubercular facets on the transverse processes decreases. The maximum width is reached and maintained at about 56 mm from the posterior cervicals through the 14th thoracic vertebra; on the 15th thoracic the width decreases to about 53 mm and on subsequent vertebrae continues to decrease until at the seventh lumbar it measures 44 mm. In these and other proportions the lumbar vertebrae of *Cynognathus* resemble those of *Thrinaxodon*. Only in the narrow, somewhat more fusiform shape of the lumbar neural spines of *Cynognathus* is there any significant difference from *Thrinaxodon*.

Sacral Series

MORPHOLOGY. Only three sacral vertebrae are preserved with the type of *C. crateronotus* (BMNH R.2571); however, the length of the associated iliac blade makes it probable that there were five sacrals as in *Thrinaxodon*. Their preservation and preparation is so poor that only a superficial comparison may be made with the sacrals of *Thrinaxodon*. As in the latter, the sacral centra are about the same length as those of the lumbar region, but tend to be narrower and more constricted about the middle. The transverse distance between prezygapophyses is much reduced, approximately 15 mm compared with 25 mm at the seventh lumbar, and the zygapophyseal facets are inclined nearly vertically. The transverse distance between the distal ends of the transverse processes is only slightly reduced, 41 mm, or 3 mm less than at the seventh lumbar. In cross-section the transverse processes are much less robust than in the lumbar series. Measured at the base, the heights of the seventh lumbar and first sacral transverse processes are 33 mm and 26 mm, respectively; the respective anteroposterior lengths are 19 mm and 14 mm. The second and third sacral vertebrae are even smaller in these dimensions. All of these features are comparable to those developed in *Thrinaxodon* sacrals. No significant differences were detected.

Caudal Series

MORPHOLOGY. Associated with the type of *C. crateronotus* are four and one-half vertebrae which probably are part of the caudal series. The centra are markedly shorter and narrower than those of the sacrum and it therefore seems unlikely that these represent the most anterior caudal vertebrae. Like the caudal vertebrae of *Thrinaxodon* the zygapophyseal articulations are oriented within 10°–20° of the sagittal plane. The transverse processes are all lost.

The exact number of caudal vertebrae in larger cynodonts such as *Cynognathus* is unknown. A specimen (NMB R.531) tentatively referred to *Diademodon* by Brink (1955) possesses at least eight caudal vertebrae. However this specimen lacks the skull and therefore cannot be positively distinguished from *Cynognathus*. It clearly demonstrates that marked diminution of caudal vertebra size occurs among the first four vertebrae and thus this cynodont's tail was relatively short.

Cervical Ribs

MORPHOLOGY. The only known cynognathid cervical ribs are preserved with *C. crateronotus* (BMNH R.2571). These include an incomplete axis rib and ribs of the sixth and seventh cervical vertebrae.

The proximal end of the axis rib is expanded into a flat, triangular plate. Dorsally one corner is the tuberculum, which articulates with the axis transverse process. The apex of the triangle is represented by the capitulum, which has been displaced anterodorsally post-mortem. During life the capitulum probably articulated between the axis and atlas centra, as in other cynodonts, and not on the atlas centrum, where there is no facet as claimed by Seeley (1895b: 102). The third corner is a flat, blunt process projecting ventrally from the plate. From the base of the triangular plate arose the distal shaft of the rib, which is broken off in this specimen. A sharp crest crosses the external surface of the plate from the base of the shaft to the base of the capitular process. The crest appears to have been continued distally along the shaft but proximally it does not reach the end of the capitulum.

The sixth and seventh cervical ribs are substantially different from the axis rib. The proximal ends of these ribs lack the development of a triangular plate. On the sixth cervical rib the wide capitulum and tuberculum bifurcate from the shaft at approximately the same level, forming a Y-shaped structure; on the seventh the capitulum is a straight continuation of the shaft, the tuberculum diverging at an angle of almost 80°. Although poorly preserved, both capituli and tuberculi appear to be thicker and more robust than their counterparts on the axis rib. A sharp median ridge from the ventrolateral aspect of both shafts continues to the proximal end of each rib between the capitulum and tuberculum. It is apparently homologous with the similar ridge on the axis rib shaft and plate. The only tendency toward a costal plate is the slight swelling of the dorsal margin of the rib adjacent to the tuberculum. This con-

dition is suggestive of the cervical ribs of *Thrinaxodon* in which an extensive, hemicircular flange arises from the dorsal margin of the shaft adjacent to the tuberculum.

Thoracic Ribs

MORPHOLOGY. In the type of *C. crateronotus* (BMNH R.2571) the first through 11th thoracic ribs are either completely lost or are broken off immediately distal to the capitulum and tuberculum. However the general structure of the anterior thoracic ribs may be inferred from a number of isolated specimens (BPI 1675; NMB C.2710; UCMP 42729). The morphological gradients that characterize these ribs cannot be described at present. The type of *C. crateronotus* shows that the 12th through 15th thoracic ribs as well as those of the lumbar series bear costal plates.

In *Cynognathus* the anterior thoracic ribs do not bear costal plates. The rib or ribs at which the costal plate is first differentiated and subsequently comes to overlap the succeeding ribs are not known. Some isolated ribs (UCMP 42729), interpreted as belonging to the most anterior thoracics, are devoid of any structure suggestive of an incipient costal plate (Fig. 14A). In these the long capitular process is straight, makes an angle with the neck of about 45°, and widely separates the capitular facet from the tubercular facet. The proximal end of the capitular process is expanded to bear an oval or round facet. The tubercular facet is an elongate oval, the long axis of which is oriented dorsoventrally. The proximal shaft is crescentic in cross-section, being somewhat convex anteriorly and concave posteriorly. Other ribs associated with the same specimen (UCMP 42729), interpreted as belonging to the middle of the thoracic series, possess a shorter, less expanded capitular process and a distinct ridge along the center of the anterior aspect of the shaft (*r c p*, Fig. 14B, C). This ridge, together with a posterior reflection of the shaft's dorsal edge adjacent to the tubercular process, apparently represents the initial differentiation of the costal plate.

Of the posterior thoracic ribs, only the 12th through the 15th are known in *C. crateronotus*. These ribs bear well-developed costal plates that are quite different from those of *Thrinaxodon*. In size the costal plates are relatively smaller than in *Thrinaxodon* and are basically diamond-shaped (*p*, Fig. 15A). The plate may be visualized as consisting of anterior and posterior flanges separated ventrally by a ridge which represents the original rib shaft. As in *Thrinaxodon* the anterior flange is the smaller of the two. Its margin is symmetrical and thicker medially than laterally. In general the thickness of the flange decreases anteriorly, i.e., toward the anterior margin. The posterior flange is asymmetrical and separated from the shaft by a very shallow groove on the dorsal and ventral surfaces. Thus this flange is rather thin along its junction with the rib shaft and is thicker along its posteromedial margin. Like the anterior flange margin, the margin of the posterior flange is blade-like and somewhat rugose.

The orientation of the proximal part of the 12th thoracic rib, and probably those of the 9th, 10th and 11th thoracic ribs as well, is approximately transverse to the sagittal axis. The capitular process lies almost directly ventral to the tuberculum and the neck of the rib passes laterally to the costal plate. The distal shaft of the rib, emerging from the ventral surface of the plate, then passes posteroventrally. The 13th, 14th and

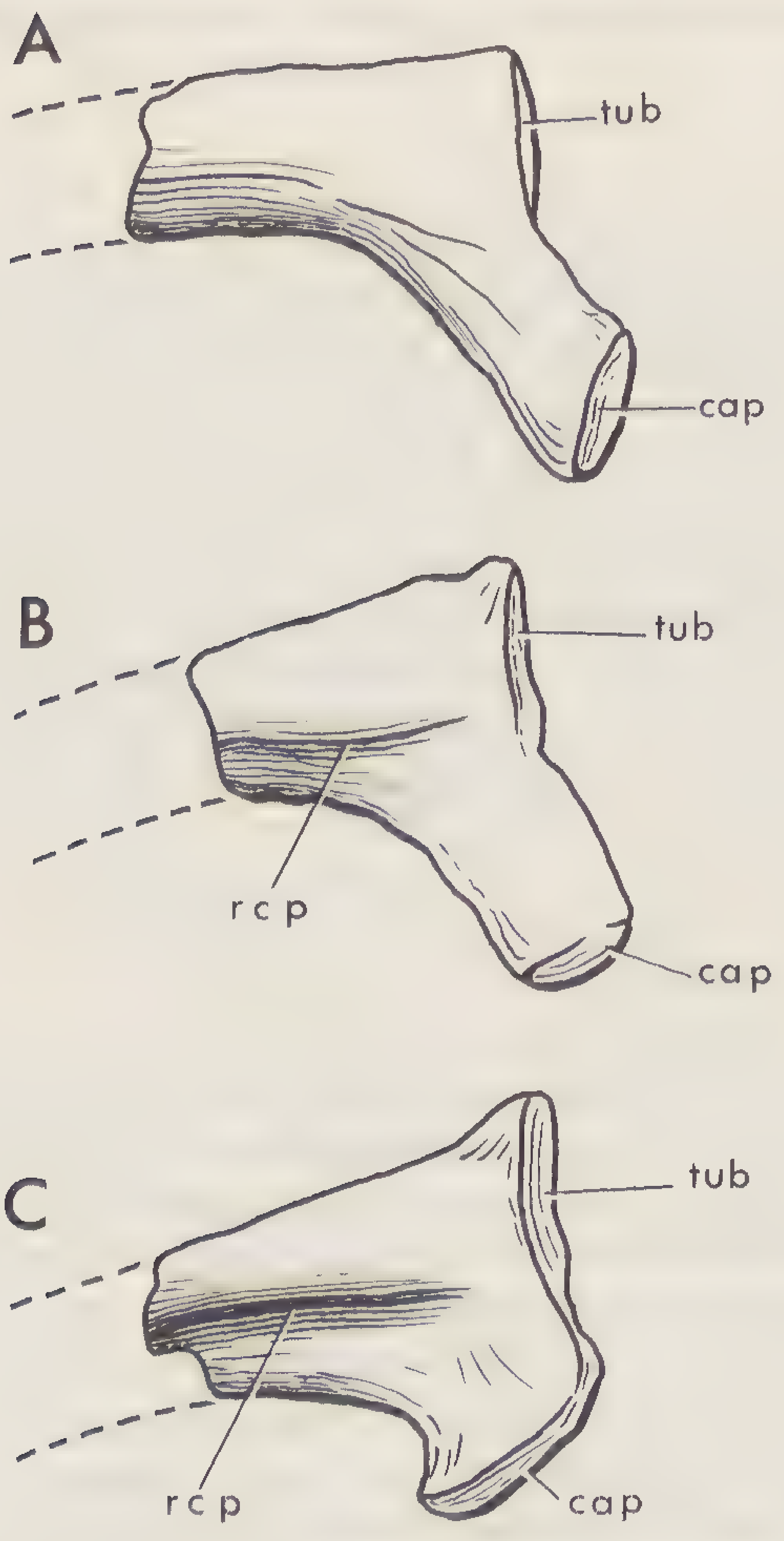

FIG. 14. Proximal ends of anterior and middle thoracic ribs of *Cynognathus* sp., UCMP 42729, in anterior view. A, B and C are interpreted as representing ribs successively more posterior in position in the thoracic series. X1. Abbreviations as in FIG. 12 except: *r c p*, ridge on anterior aspect of rib shaft representing incipiently developed costal plate.

15th thoracic ribs, however, undergo a reorientation of the neck that is carried over into the lumbar series. The neck in these ribs is directed more anterolaterally, instead of laterally (Fig. 15A). At the same time the neck is progressively modified from an anteroposteriorly narrow shaft to a broad shaft, while retaining approximately the same depth as in the 12th thoracic rib.

The costal plates of the 12th and 13th thoracic ribs develop a ridge along the posteromedial border of the dorsal surface (*r*, Fig. 15A). This ridge arises at the junction of the costal plate and the proximal part of the rib shaft and runs obliquely to the shaft axis, ending at the lateral margin of the posterior flange. On the 14th thoracic rib the position and proportions of this ridge resemble those of the costal tubercle developed in *Thrinaxodon*. On the 15th thoracic rib the ridge, here much enlarged,

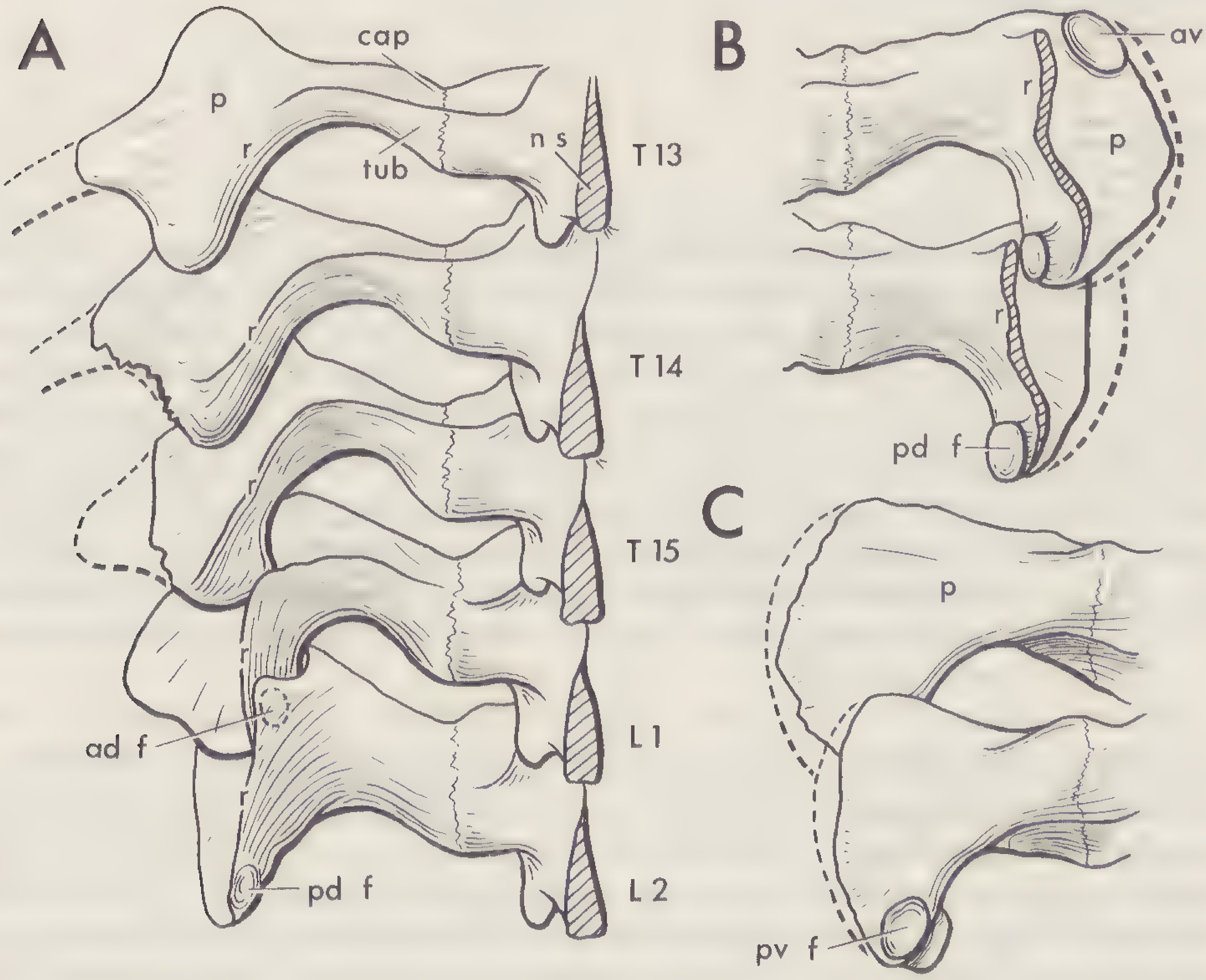

FIG. 15. Lumbar ribs of the *Cynognathus—Diademodon* pattern. A, dorsal view of thirteenth thoracic through second lumbar vertebra of *Cynognathus crateronotus*, BMNH R.2571. B, dorsal; C, ventral views of unassociated lumbar rib plates of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, showing placement of facets. Approx. X0.5. Abbreviations as in FIG. 12 except: *ad f*, anterodorsal facet; *av f*, anteroventral facet; *pd f*, posterodorsal facet; *pv f*, posteroventral facet; *r*, ridge on costal plate. For details, see text.

extends almost to the anterior edge of the plate and is more oblique to the axis of the rib shaft. On the following rib, the first lumbar, the crest of the ridge is reflected laterally to such an extent that the posterior flange of the 15th thoracic costal plate is gripped in pincer-like fashion between the ridge and the dorsal surface of the first lumbar costal plate. This arrangement is further elaborated in the lumbar region described below. It may be noted here, however, that disarticulated rib plates (especially UCMP 42729) possess slightly raised, oval articular facets at the points of plate overlap; this feature, too, is repeated in the lumbar series.

In the type of *Cynognathus* the 14th and 15th thoracic ribs are synostosed to their transverse processes along distinct, serrate sutures. The 12th and 13th thoracic ribs are probably synostosed. The shafts of the 10th and 11th thoracic ribs are broken across the neck, although the capituli and tuberculi still are articulated, and it appears possible that these ribs were also synostosed. The presence of adherent matrix on the type, especially at the rib articulation of the 10th and 11th thoracic ribs, makes the nature of the articulation difficult to interpret. However the transition from unfused ribs in the

middle thoracic series to fused ribs in the posterior thoracic series is analogous to the condition in *Thrinaxodon*.

Lumbar Ribs

MORPHOLOGY. The lumbar region is distinguished from the thoracic on the basis of rib morphology. The first lumbar vertebra is here defined as the first dorsal vertebra bearing a costal plate that grips the preceding costal plate, i.e., the 15th thoracic, by a lateral reflection of its dorsal ridge (*r*, Fig. 15A). In addition, all lumbar ribs lack shafts or shaft vestiges distal to the costal plate. However, the morphological transition between thoracic and lumbar ribs is gradational. The decision as to which costal plate first achieves the interlocking mechanism and loses the distal rib shaft is somewhat arbitrary as Figure 15A shows; during lateral flexure the 15th thoracic rib obviously might interlock with the 14th thoracic rib. Nevertheless the lumbar and thoracic series are quite distinct with respect to rib morphology, despite their intergradation, and deserve separate recognition.

The articulation between successive lumbar costal plates involves at least three and probably four articular facets. These can be seen only in disarticulated material from which all matrix has been removed. An anteroventral facet (*av f*, Fig. 15B), facing dorsally and slightly laterally, articulates with a posteroventral facet (*pv f*, Fig. 15C) of the next rib plate in front. Between the same two plates there is also a posterodorsal facet (*pd f*, Fig. 15A, B), facing dorsally and slightly medially, which must contact another facet not yet seen because of incomplete or matrix-cemented specimens. The "unknown" anterodorsal facet (*ad f*, Fig. 15A) must occur on the ventral side of the laterally reflected ridge, which is broken off in the specimens in Figure 15B. Since no disarticulated and associated lumbar plates are available, it is impossible to make an accurate estimate of the movements permitted. The small size of the facets is evidence that lateral movements, at least, could not have been great.

Essentially the same mechanism of lumbar rib articulation is known in a Middle Triassic cynodont from Tanzania (see ?*Aleodon*-?*Scalenodon*, BMNH TR.8).

The capitulum and tuberculum of each lumbar rib are conjoined and cannot be distinguished except by position. The neck of the lumbar ribs becomes successively shorter so that the seventh lumbar plate is differentiated closer to the midline than that of the first lumbar. This shift is also augmented by a successive shortening of the synapophyses.

6. THE POSTCRANIAL AXIAL SKELETON OF *DIADEMODON*

MATERIAL. *Diademodon*, the best known gomphodont in terms of cranial morphology and dentition, is in fact poorly known in terms of the postcranial axial skele-

ton. At present there is only one reasonably complete axial skeleton that can be positively assigned to this genus (USNM 23352). This specimen, of rather friable bone encased in an unusually tenacious matrix, provides a very limited amount of information. Other specimens include *Microgomphodon eumerus* (BMNH R.3581), originally described by Seeley (1895a) and subsequently recognized by Brink (1955) as possibly a juvenile *Diademodon* sp. Broom (1905a) described a single vertebra, apparently from the lumbar series, of a cynodont positively identified as *Diademodon.* Broili and Schröder (1936) gave a fairly complete account of several thoracic and five articulated lumbar vertebrae from a specimen tentatively identified as *Gomphognathus* (= *Diademodon*). More recently Brink (1955) drew up a skeletal reconstruction of *Diademodon*, modeling the postcranial axial skeleton primarily on NMB 531. This particular specimen cannot be positively identified as *Diademodon*, as Brink acknowledged, because it lacks the skull. Furthermore Brink's illustration of the actual fossil does not adequately portray the fact that many features have been reconstructed in plaster or are otherwise lost or obscured. Until more complete and better preserved remains of a positively identified *Diademodon* are available, there is little morphological or comparative data that can be stated with confidence.

MORPHOLOGY. Assuming that NMB 531 is a *Diademodon*, then this genus has at least 30 presacral vertebrae—three more than *Thrinaxodon* and one more than the type of *Cynognathus crateronotus*. The sacrum includes five vertebrae, as in *Thrinaxodon*. Brink (1955: 25) stated that there are only four sacrals in NMB 531, but he overlooked the fact that the rib of the fifth sacral is directed anterolaterally and probably contacted the ilium as in galesaurids. Thus the tail, as preserved in this specimen, has eight vertebrae.

Anapophyses, which are well developed in the cervical series of galesaurids, are apparently lacking in this region in *Diademodon* as they are in *Cynognathus*. Elsewhere they are typically developed. It appears likely that in general morphology and proportions the vertebrae of *Diademodon* are quite comparable to those of *Cynognathus*.

Of particular interest are the costal plates. Brink's (1955) reconstruction of *Diademodon* portrayed the lumbar plates as having a basically galesaurid pattern, i.e., more or less rectangular with a simple imbricating relationship (see Fig. 12C). However USNM 23352, whose generic identity is certain, has lumbar costal plates which are cynognathid in pattern (see Fig. 15). Brink (1955: 25) also states that "the lumbar ribs of *Diademodon* are essentially similar to those of *Cynognathus*." But Brink's reconstruction depicts greater dissimilarity than actually exists. In fact as yet there are no known characters of the lumbar ribs with which to distinguish these two genera. In the middle and anterior thoracic region, however, there is a possible difference between the *Diademodon* and *Cynognathus* rib morphology. In the latter there are either no costal plates or costal plates that are only incipiently differentiated. Brink reconstructs *Diademodon* as having small but nonetheless well-defined costal expansions on all anterior and middle thoracic ribs. The evidence for this in NMB C.531 and in USNM 23352 is equivocal.

7. THE PROBLEM OF EXPANDED RIBS IN CYNODONTS

Critique of Previous Theories

A number of paleontologists have studied cynodont costal plates and speculated upon their functional significance. Their conclusions offer a variety of alternatives. In the following section an attempt is made to evaluate each of the previously proposed theories in terms of the comparative skeletal data presented above.

Seeley (1895b), who originally described *Cynognathus*, did not speculate on the function of the ribs' peculiar morphology except to note that he had not seen any animal, fossil or recent, with a comparable structure.

Gregory and Camp (1918: 540–544) gave a reconstruction of *Cynognathus* and were the first to consider the plates in terms of the living animal. They proposed two hypotheses: first, that "the peculiar characters of the lower dorsal and lumbar ribs are possibly connected with an extremely large size and powerful musculature of the head which might require an equally strong development of axial musculature," and second, that "the sharp differentiation of the dorsal and lumbar region may also indicate that the muscular complex forming the diaphragm [had evolved]." With regard to the first hypothesis, Gregory and Camp do not show why muscular compensation for a heavy head must occur in the lumbar region. In both mammals and reptiles specializations to suspend a large or bulky head invariably occur in the anterior thoracic and cervical regions. This fact considerably undermines the credibility of their first theory.

Gregory and Camp's second theory is more concerned with lumbar and thoracic rib differentiation than with the function of the costal plates. The lack of extensive rib shafts in the abdominal region of cynodonts is an interesting parallel to the mammalian condition and is possibly related to the development of a diaphragm. However this condition cannot be construed as evidence for a diaphragm because there are also reptiles in which the posterior dorsal ribs are either much reduced in size or are represented only by the fused extremities of the transverse processes, i.e., crocodilians. Recognizing the possibility that cynodonts possessed a diaphragm, Gregory and Camp nevertheless do not attempt to relate it to the function of the costal plates. Further criticism of the diaphragm theory is given below with reference to Brink's hypothesis.

Haughton (1924: 90–93), the next author to consider the function of costal plates in cynodonts, unfortunately made no attempt to relate his three hypotheses of costal plate function to his analysis of muscular anatomy. Haughton's first and second hypotheses were that the plates must have added strength to the back and at the same time acted as a protective shield analogous to dermal plates or a carapace. Broom (1932b: 263) also "suspects that a small carapace of fibrous tissue has covered the lower dorsal and lumbar regions." The imbricating arrangement of plates undoubtedly strengthened the back, but Haughton did not elaborate as to exactly how this was accomplished or for what possible adaptation. Cynodont costal plates are hardly analogous to a carapace for, as Haughton himself admitted, the plates probably

were covered with well-developed muscles. No dermal ossifications or "carapace" plates have ever been found. While protection may have been a secondary advantage of these plates, there is no evidence to suggest that it was the primary selective factor in their formation.

Haughton's third hypothesis, that the costal plates prevented dislocation during lateral flexure, was based upon the supposition that "more or less sudden bending may have been necessary if . . . [the cynodonts'] food consisted largely of insects." However the interdependence of an insectivorous diet and abrupt lateral flexure of the axial skeleton is by no means established. Certainly not all cynodonts possessing costal plates were insectivorous. Moreover the design of plates did not prevent an animal such as *Thrinaxodon* from assuming a very tightly curled position (Brink, 1958) such as is common among modern mammals when resting. Costal plates therefore could not have acted as a "stop" to prevent lateral flexion. The degree of lateral flexion preserved in the specimen described by Brink is far in excess of what might be reasonably expected in locomotion or in feeding behavior.

Despite the inadequacies of these hypotheses,[8] Haughton's observation that the costal plates possibly served for iliocostalis insertion is of interest, particularly with regard to an analogy drawn by Williston (1925: 115). In his *Osteology of the Reptiles* Williston remarked that the expanded ribs of *Cynognathus* "gave great strength to the lumbar region, and are perhaps analogous to the greatly expanded transverse processes of the crocodiles." The meaning of the last observation is left unexplained, but presumably refers to a lever-like action of epaxial muscles on the long, laterally directed transverse processes. The functional significance of Haughton's and Williston's observations will be considered in following sections.

Brink (1954: 121) proposed that cynodont costal plates developed in conjunction with the evolution of a diaphragm. He elaborated his views with reference to *Diademodon* (1955: 27–28), and again in greater detail with reference to cynodonts in general (1956: 78–84). Brink reiterated Gregory and Camp's (1918) observation that the trunk may be divided into thoracic and lumbar regions on the basis of rib differentiation; the reduction or absence of abdominal ribs permits visceral displacement in response to a contracting diaphragm and is apparently a necessary condition for a diaphragm. However since many reptiles also have reduced ribs or lack them altogether in the posterior dorsal series, thoracolumbar differentiation in mammal-like reptiles is a rather equivocal piece of evidence for a diaphragm. Despite the fact that the presence of a diaphragm in cynodonts is as yet unproven, Brink further speculated that "at this stage the intercostal muscles apparently failed to act as effective antagonists to the diaphragm," necessitating overlapping ribs to maintain the integrity of the thorax. In several respects Brink's hypothesis is untenable. First, the presence of costal plates on *all* presacral ribs in galesaurids is difficult to relate to stresses generated by a diaphragm—stresses which in the cervical and posterior lumbar regions must have been negligible or nonexistent. If costal plates were an adaptation to such stresses, then in later cynodonts (*Cynognathus, Diademodon*), in which reduction of the plates occurs, the retention of plates in the thoracic region would be expected. Instead the

[8] For other criticisms see Brink (1954: 119).

costal plates of later cynodonts are lost in all thoracic vertebrae except the most posterior and are much elaborated in the lumbar region where diaphragmatic action requires that the visceral cavity be the most distensible. Thus the claim that costal plates arose in response to stresses induced by a diaphragm is supported neither by any biomechanical facts nor by the skeletal distribution of the plates themselves.

Secondly, there is no evidence to support Brink's (1955: 27) assumption that the intercostal muscles of cynodonts were ineffectual. If indeed the intercostal muscles were inadequate to sustain the intracavitary stresses induced by the diaphragm, the question arises as to why the imbrication of ribs did not extend the entire length of the ribs. Brink's further speculation (1956: 84) that a "largely involuntary diaphragm and fully voluntary intercostal muscles in the Cynodontia could not be brought to well timed cooperation" is without foundation.

Brink's (1955: 27) observation that the lumbar costal plates of *Diademodon* prevented intervertebral rotation is unquestionably valid. Brink further argued that the reduction or loss of thoracic costal plates in *Diademodon* might possibly relate to the necessity of intervertebral rotation, "twisting of the torso" in Brink's terminology, during respiration or locomotion or both. However, even if the costal plate structure is disregarded, intervertebral rotation between dorsal vertebrae of any known cynodont would have been impossible because of the zygapophyseal articulations and the anapophyses. To permit intervertebral rotation, zygapophyses must conform to a radius of a circle, the center of which lies approximately at the nucleus pulposus. In *Thrinaxodon*, *Diademodon* and *Cynognathus*, zygapophyseal orientations in the dorsal vertebral series vary from almost parasagittal to nearly horizontal, thus obviating the possibility of intervertebral rotation. The close fit of each anapophysis into the groove on the next posterior pedicle is another interlocking mechanism which would also prevent rotation. It is difficult to argue convincingly that the prevention of intervertebral rotation, whether during locomotion or respiration, was the prime function of costal plates when the typical adaptations to resist such movements are well developed in the vertebral column.

The Relation of Costal Plates to Epaxial Muscles: A Comparative Review of Epaxial Musculature

The obvious interpretive approach to the problem of an unusual skeletal feature is through reconstruction of non-skeletal anatomy. Muscle patterns and their relation to posture and locomotion are important influences on postcranial bone morphology, and therefore are more likely to be related to an unusual skeletal feature than are other aspects of the soft anatomy.

Cynodont costal plates are located on the proximal half of the ribs, approximately at the point where an angle would be expected. The only supracostal musculature which is continuous along the trunk and neck at this level is the epaxial system. Gregory and Camp (1918) and Haughton (1924) first suggested that the epaxial muscles were involved with costal plates, but failed to explore the possibility. In order to determine the possible distribution of epaxial muscles in cynodonts, a comparative survey of the epaxial muscles in living reptiles and mammals must be made.

THE EPAXIAL MUSCULATURE OF REPTILES

The general plan of reptilian epaxial musculature is tripartite, being divisible into a medial (transversospinalis) system, an intermediate (longissimus) system, and a lateral (iliocostalis) system. Variation can be expected within this basic framework, for reptiles are diverse in habit and locomotion. Some variations reported in classical accounts of reptilian epaxial musculature are merely terminological, while others reflect differences in the detail of dissection. Nevertheless all accounts agree with Vallois' (1922) observation that the transversospinalis, longissimus and iliocostalis systems constitute the basic and primitive reptilian epaxial arrangement.

The transversospinalis system consists of a diverse series of small muscles which are primarily intervertebral but which may also span two or more vertebrae. In *Iguana* (Olson, 1936), for instance, the Mm. interspinalis between adjacent neural spines are inseparable from the Mm. interarcuales between adjacent neural arches. The Mm. interarticulares are distinct, linking adjoining postzygapophyses and having accessory attachments to the prezygapophyses. The Mm. intertransversarii link adjacent transverse processes along their dorsal aspect. The Mm. levator costae, when present in other reptiles, usually arise on the posterior (ventral) surfaces of the transverse processes and insert on the capitular process of the next posterior rib. In *Iguana* these muscles are reduced in size and limited to a few cervical vertebrae.

In addition to short intervertebral muscles there are commonly longer fascicles which span the lengths of two or more vertebrae. These are commonly termed the Mm. spinalis, which arise and insert on the neural spines or their bases and the Mm. semispinalis, which arise on the neural spines but insert either into the dorsal intermuscular septum, separating the transversospinalis and longissimus systems, or into the longissimus system itself. In *Iguana* the Mm. spinalis are represented by a series of small tendons which arise from the base of the spine, pass posteriorly over four vertebrae and insert on the spine of the fifth (Olson, 1936). The Mm. semispinalis arise in continuity with these tendons and insert on the dorsal intermuscular septum.

A primitive or even general pattern of transversospinalis musculature is not easily discerned from available studies of living reptiles. The apparent diversity is no doubt in part due to differences in nomenclature and detail of dissection. However Vallois (1922), in a monographic study of the epaxial musculature of vertebrates, presented evidence that a basic transversospinalis pattern is recognizable in each of the living orders of reptiles, Chelonia excepted. This pattern consists of three distinct groups of fascicles: Mm. spino-articularis, articulo-spinalis and interspinalis. The spino-articularis arises on the zygapophyses and passes posteromedially to insert on a neural spine one or more vertebrae caudal to the origin. The articulo-spinalis runs in the opposite direction; it arises from the zygapophyses and passes anteromedially over one or more vertebrae to insert on a neural spine cranial to the origin. The interspinals, as the name implies, are confined in attachment to the neural spines and also to the neural arches.

The tripartite division of the transversospinalis is somewhat of an oversimplification, as Vallois recognized. Other systems of fascicles, e.g., interarticular and intertransverse muscles, are present in some orders but not in others. Nevertheless there is a

basic pattern to the transversospinalis systems and it may best be described in terms of three laminae. The most lateral and superficial system is the articulo-spinalis (sensu Vallois), running anteromedially from zygapophyses to neural spines. Medial and deeper to this is the spino-articularis (sensu Vallois), running posteromedially from zygapophyses to neural spines. Most medial and deepest of all is the interspinalis group; in addition to the interspinal fascicles present in all living reptilian orders, excepting Chelonia, this group may include muscles which span the arches (interarcuales), the zygapophyses (inter-articulars), the transverse processes (intertransverse muscles) as well as the ribs and transverse processes (levator costae). In addition the interspinal group may include specialized derivatives of this system not found in other reptilian orders.

Olson (1936) implied that the medial, posterodorsally directed spino-articularis system[9] is the primitive arrangement, and that the lateral, anterodorsally directed articulo-spinalis system[9] was differentiated later in tetrapod evolution. There is, in fact, no substantial evidence for this claim other than Olson's interpretation of the direction of spinalis and semi-spinalis fascicles in primitive fossil forms. While the muscle scars give evidence of the presence of such fascicles, they do not permit certain interpretation of their direction, i.e., whether anterodorsal or posterodorsal.

It seems likely that the spino-articularis and articulo-spinalis fascicles of the transversospinalis are derivatives of a primitive, metameric epaxial system adjoining the vertebrae. Yet much of transversospinalis system in living reptiles is intervertebral, i.e., between adjacent vertebrae, and thus preserves the primitive, metameric pattern. In general, however, the evolution of the epaxial muscles involves the loss of myoseptal divisions and the development of fascicles spanning many vertebral segments (Vallois, 1922; Olson, 1936). The lateral parts of the reptilian transversospinalis system, i.e., the spino-articularis and articulo-spinalis, participate in this trend and in many reptilian groups may span three or more vertebrae. This trend is still only incipiently developed in reptiles, while in mammals the primitive metameric pattern is thoroughly modified.

The intermediate epaxial group is the longissimus system, and in the trunk it is one muscle, the M. longissimus dorsi. In *Iguana*, as in most living reptiles, this muscle is bounded medially by a dorsal intermuscular septum (Olson, 1936). It takes origin from this septum, as well as from the dorsal edge and medial surface of the ilium, the sacral ribs, and the prezygapophyses of the dorsal vertebrae. It inserts on the transverse processes and proximal rib shafts. The longissimus dorsi is bounded laterally by the lateral epaxial system, the M. iliocostalis dorsi. In *Sphenodon* and most other reptiles, the arrangement is basically the same (Vallois, 1922).

The lateral epaxial group is the iliocostalis system and in the trunk it is a single muscle, the M. iliocostalis dorsi. In *Iguana* this muscle takes origin from the dorsal edge and medial surface of the ilium and by tendons from the M. longissimus dorsi (Olson, 1936). It has a tendinous insertion into the dorsal aspects of the ribs (ibid.). The longissimus dorsi of *Sphenodon* and other reptiles is arranged in a fundamentally similar manner, commonly attaching to intermuscular septa (see Vallois, 1922).

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[9] Olson (1936) referred to these as the spinalis-semispinalis system which has two fiber directions. The difference is only in nomenclature.

THE EPAXIAL MUSCULATURE OF MAMMALS

The epaxial musculature of mammals retains the tripartite arrangement of reptiles. The transversospinalis, longissimus and iliocostalis systems bear similar relationships to each other although individually they display specializations in response to a basically different mode of locomotion.

Slijper (1946: 46; fig. 37) suggested that there is a fundamental difference between mammals and reptiles in the proportions of the transversospinalis and iliocostalis systems. In reptiles the iliocostalis musculature is proportionately larger than the transversospinalis because its lateral position is more mechanically suited to effect the undulatory movements of locomotion than either the longissimus or transversospinalis, which lie medially. In mammals, locomotion involves movement of the spinal column primarily in a sagittal plane and consequently the transversospinalis system is proportionately larger and more differentiated.

Slijper's (1946) comparative data on the epaxial musculature of 80 species of mammals establishes a sound base on which to construct general conclusions about mammalian epaxial patterns, regardless of functional interpretations. The following outline of the mammalian epaxial pattern is based primarily on Slijper's work.

The transversospinalis system, as in reptiles, contains a number of different series of muscles. The terminology of these muscles varies greatly in the literature, largely because the muscles themselves are so diverse in attachment and segmentation that they defy a comprehensive system of classification. The definitions of mammalian transversospinalis muscles given by Slijper (1946: 52) are broadened here so as to include obvious variations. The M. spinalis is a series of fascicles between neural spines and usually spans at least two and usually more vertebrae between origin and insertion. Spinalis fascicles are sometimes intergrown with the M. semispinalis; they originate at the neural spines or a lateral equivalent such as the fascia of the M. longissimus dorsi and pass posteroventrally to the zygapophyses or metapophyses of usually the fourth or more vertebra caudal to the point of origin. The Mm. multifidus, rotatores longi, and rotatores breves are successively more medial (deeper) series which have the same attachments as the M. semispinalis. The M. multifidus spans two, and in some cases three vertebrae, to be inserted into the third or fourth vertebra caudal to the origin. Similarly the Mm. rotatores longi and breves insert into the second and first vertebrae, respectively, caudal of their origin. In addition to these muscles, the M. interspinalis spans the neural spines of adjacent vertebrae as in reptiles. The Mm. intermammillares, or interarcuales of other authors, link adjacent vertebrae by passing between neural arches or metapophyses. Mm. intertransversarii attach to successive transverse processes.

In terms of fascicles connecting major elements or processes of the vertebral column, mammals are not significantly different from reptiles except in one respect. There is a conspicuous absence of semispinalis fascicles running posterodorsally, i.e., from the neural arches or metapophyses posteriorly to the neural spines (Slijper, 1946: 52). The M. semispinalis of mammals runs only from the neural arches or metapophyses cranially to the neural spines.

While the components of the transversospinalis system remain much the same between mammals and reptiles, the arrangement of these components differs considerably. In a few mammals the transversospinalis is undifferentiated throughout the length of the trunk. Semispinalis, multifidus and other shorter fascicles are fused. This occurs primarily in animals with specialized modes of locomotion (Slijper, 1946: 53, table 3) and may be regarded as atypical. For all other mammals it is possible to make two generalizations concerning the transversospinalis system. First, the system tends toward the regional specialization of muscles associated with the thoracic ("prediaphragmatic region" of Slijper) and lumbar ("post-diaphragmatic region" of Slijper) series. This differentiation takes a wide variety of forms, but principally the differences are either in the presence or absence of one or more subdivisions of the transversospinalis, or their fusion into one or more undifferentiated muscle masses (see Slijper, 1946, table 3 for comparative data). Second, the spinalis and semispinalis tend to develop long fascicles which originate in the thoracic and insert in the lumbar region (ibid.: 53–54). Slijper implies—incorrectly—that the differentiation of the transversospinalis system into its various components is a peculiarity of mammals. Reptiles possess muscle fibers which are in basically the same relation to the axial skeleton as are the components of the mammalian transversospinalis system. The primary difference is not that the transversospinalis of mammals is more completely divided into constituent muscles, although this may be true in part, but it is more specialized morphologically in relation to regions of the axial skeleton. This differentiation is reflected in the distinct morphology of mammalian thoracic and lumbar vertebrae, as well as relatively large morphological changes between individual vertebrae. In reptiles the transversospinalis tends to be more uniformly developed throughout the trunk and associated with this is a relatively undifferentiated axial skeleton.

The mammalian longissimus system resembles that of reptiles in its origin from the proximal rib shafts and transverse processes and its partial insertion into the ilium.[10] Here the similarity ends, however. The rest of the inserting fibers tend to displace from the metapophyses to the spinal apices of sacral, lumbar and, more rarely, posterior thoracic vertebrae (Slijper, 1946: 49). This shift probably allows the longissimus to act synergistically with the transversospinalis system, at least with respect to sagittal movements of the lumbosacral region. Furthermore the longissimus is commonly characterized by long fascicles which originate in the thoracic and insert in the lumbar region (ibid.).

The iliocostalis system, with a few specialized exceptions, is relatively narrower and smaller in mammals than in reptiles (Slijper, 1946: 46). Like the longissimus system, it characteristically has long fascicles but may, in the thoracic region, retain shorter fascicles which approximate a metameric condition (ibid.). In particular the iliocostalis tends to separate into an M. iliocostalis thoracis and an M. iliocostalis lumborum. The latter is usually found to be fused in a variable degree with the longissimus by means of a dense, sheet-like aponeurosis extending from the midline laterally over the dorsal area; the combined musculature is known as the M. erector spinae. This ar-

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[10] Slijper (1946: 49) incorrectly stated that the reptilian longissimus dorsi does not insert on the ilium. For numerous examples that contradict this assertion, see Maurer (1899), Romer (1922b) and Olson (1936).

rangement is a further development of the mammalian trend to develop musculature for sagittal movement or fixation of the spinal column.

The foregoing review of epaxial muscles in living reptiles and mammals has emphasized that the two classes share a common tripartite pattern of back musculature. In reptiles much of the primitive, metameric pattern is retained—despite specializations and the tendency to parallel the mammalian development of longer fascicles. Associated with their comparatively primitive myology is a relatively undifferentiated axial skeleton. The iliocostalis is commonly the largest of the epaxial muscles, a correlate of locomotion involving lateral undulation. In mammals the axial skeleton is highly differentiated and so also is the epaxial musculature. The transversospinalis is well developed and, together with the specialized erector spinae, contributes to the ability to effect sagittal movements important to locomotion. With these considerations in mind, it is now possible to make a functional evaluation of the axial skeleton of *Thrinaxodon*.

Reconstruction of the Epaxial Musculature in Thrinaxodon

In living reptiles and mammals the epaxial musculature is tripartite and it may be confidently assumed that the arrangement was similar in *Thrinaxodon*. The most medial of the three, the transversospinalis system, will be considered first.

The transversospinalis of *Thrinaxodon* was probably confined, as in living tetrapods, to the space medial to the distal ends of the transverse processes. The repetitious uniformity of the dorsal vertebrae is evidence that this muscular system was more similar to the reptilian than to the mammalian pattern. In mammals many of the components of the transversospinalis are restricted to or are differently developed in various segments of the spinal column. This is associated with functional differentiation of vertebral regions (thoracic, lumbar, etc.) as well as with rather sharp morphological gradients between adjacent vertebrae. No such differentiation is evident in *Thrinaxodon*. Thoracic and lumbar vertebrae are remarkably uniform. In lateral aspect the spines and arches form smooth, non-angular surfaces which are not interrupted by large metapophyses or muscle scars. The undifferentiated vertebral morphology is evidence that the muscular structure retained a primitive metameric pattern. Moreover the neural spines are relatively short and thus provide neither the height nor the leverage for a strong transversospinalis system capable of producing effective sagittal flexure.

In *Thrinaxodon* the Mm. interarcuales and interarticulares were probably not differentiated because their areas of attachment are smoothly confluent. Minute metapophyses on the postzygapophyses of the dorsal vertebrae (*m*, Fig. 12A) indicate that the Mm. interarticulares may have been partly tendinous. The anterior margin of each dorsal neural spine, except those of the first two thoracics, extends nearly to the posterior margin of the next vertebra. The anterior margin, being extremely thin, is frequently broken, but in several fairly complete specimens it is clear that the anterior margin of each neural spine was accommodated in a vertical recess in the posterior margin of the preceding spine. There was obviously no contact between adjacent

spines, but the extremely close proximity effectively prevented any extensive sagittal flexion. As a result the M. interspinalis in the thoracolumbar region was probably poorly developed and perhaps entirely replaced by an interspinous tendon.

The Mm. Levator costae, running from the posteroventral aspect of the transverse processes to the next posterior rib, were probably well-developed. The insertions on the anterior aspect of the shafts between the capitulum and tuberculum are marked by rugosity and a slight tuberosity or crest. The probable area of origin lies on the posteroventral surface of each transverse process and on the continuation of this surface onto each tuberculum. Together these surfaces form a concavity which becomes progressively deeper posteriorly (*cp*, Fig. 12B). The concavity bears a moderate amount of rugosity, especially along its dorsal rim. The development of large Mm. levator costae, as interpreted from these areas of attachment, relates to the production of lateral flexure of the vertebral column. With the ribs fixed either by synostosis with the vertebrae, in the lumbar series, or by union of the costal cartilages to the sternum, in the thoracic series, tension between transverse processes and ribs would tend to cause rotation of the vertebrae, and hence lateral flexure of the column. It is certain that the Mm. intertransversarii between adjacent transverse processes could have produced such movement and it is probable that the Mm. intertransversarii and levator costae were closely associated functionally if not actually a single muscle mass. Therefore the most strongly developed part of the transversospinalis system in *Thrinaxodon* is situated to produce lateral, not sagittal, movements of the vertebral column.

It is possible that the transversospinalis muscles associated with the cervical and first four thoracic vertebrae were more differentiated than the simple, metameric muscles of the trunk. The elongate, narrow spines of these vertebrae differ from each other in the degree of recurvature and apical thickness. Such variation is evidence of differences in stress and muscular attachment. Their height permits deeper and hence stronger transversospinalis musculature than in the thoracolumbar region. Both height and recurvature provides advantageous leverage for Mm. multifidus and rotatores, as well as for the longer spinalis or semispinalis musculature. In most reptiles, however, the cervical vertebrae are in some degree modified by the special requirements of suspending the head and both the transversospinalis and longissimus systems tend to develop long fascicles. The differentiation of cervical vertebrae in *Thrinaxodon* cannot be considered as a strictly mammalian feature because both reptiles and mammals respond to the problem of head suspension by specialization of the cervical vertebrae and muscles. Nevertheless, with the possible exception of the anterior thoracic and cervical regions, the transversospinalis system of *Thrinaxodon* appears to have retained the primitive, basically metameric structure of a reptilian grade.

In *Thrinaxodon* the longissimus system occupied a wide, parasagittal trough along the dorsal aspect of the axial skeleton, an interpretation shared with Haughton (1924) and Brink (1954). This trough is bounded medially by the neural spines (or transversospinalis musculature during life), ventrally by the transverse processes and ribs, and laterally by the upturned costal tubercles. Its position is analogous with the longissimus position among most living tetrapods in which, of course, no trough is developed. The "floor" of the trough is discontinuous by virtue of the intercostal spaces. It is deepened laterally by the emargination (*gr*, Fig. 12A) of the dorsal aspect of the rib shafts. In the posterior lumbar vertebrae the transverse processes are also emarginate

distally, thus broadening the trough near the sacrum. Emargination of sacral ribs is well-developed on the first two, less developed on the third and fourth, and absent on the fifth. The development of the trough is explicable in terms of providing space for an enlarged M. longissimus dorsi. If, as in living reptiles and mammals, the longissimus system in *Thrinaxodon* took origin from the sacrum, from the medial surface and dorsal edge of the iliac blade, and from the transversospinalis fascia, then this musculature must have been relatively well developed because these surfaces are extensive. The likely points of insertion—the transverse processes and medial surfaces of the costal tubercles—also form an extensive surface area which is consistent with a large muscle mass. The grooved dorsal surface of the ribs medial to the costal tubercles appears to have accommodated the belly of the longissimus from which inserting slips may have branched on either side. It appears probable that the longissimus system in the trunk was composed of a single, non-segmented muscle mass. Metameric segmentation, if present, would have been delineated in part by tendinous myosepta (myocommata) for which there is no evidence (for evidence of myosepta in fossil forms, see Olson, 1936). Furthermore, metameric segmentation would not account for the emargination of the ribs which creates a continuous trough from the sacrum to the anterior thoracic vertebrae.

The M. longissimus dorsi as interpreted in *Thrinaxodon* is a well-developed muscle running the length of the trunk. Unilateral contraction of this muscle would laterally flex the spinal column. The efficiency of such action was apparently augmented in the lumbar region by fusion of the ribs to the transverse processes. Lumbar ribs act as extensions of the transverse processes and are analogous to lateral levers. In mammals, for instance, the neural spines are lengthened to function more efficiently as sagittal levers (Slijper, 1945: 79 ff.). The principle is the same in *Thrinaxodon*, except the levers are arranged to transmit lateral forces.

The transition from mobile to immobile ribs is in the posterior thoracic vertebrae. The efficiency of mobile ribs as levers was probably diminished only slightly because the capitulum and tuberculum are robust structures and retain extensive contact with the vertebrae. Furthermore the capitulum is located anteroventral to the tuberculum. This arrangement would permit rib movement anterodorsally or posteroventrally, with the center of the capitulum and tuberculum acting as hinge points. However, the overlapping costal plates prohibit such movement and therefore eliminate the only possibility for significant rib movement independent of the vertebrae.

In the anterior thoracic series the longissimus trough is narrower, suggesting that here the muscle was smaller and lateral flexure perhaps less extensive. The capituli and tuberculi of anterior thoracic ribs lie in a more or less vertical relationship and the costal plates are nearly vertical. This arrangement would permit limited costal movement, probably associated with respiration, if the distal ends of the shafts were not immovably joined to the sternum.

The iliocostalis system, the most lateral of the epaxial musculature, probably occupied the external (dorsal) surfaces of the costal plates in the trunk and neck. As is common in most tetrapods, its extent would be interrupted by the ilium, although the more medial longissimus system might be continuous over the sacrum into the caudal series. The caudal iliocostalis system was probably represented by the lateral part of the M. extensor caudae lateralis, as in *Iguana* (Olson, 1936).

There is no osteological evidence as to whether the M. iliocostalis dorsi was a series of metameric muscular bundles between adjacent costal plates or was a single belly with multiple attachments. Metamerism of the trunk iliocostalis is retained by many living reptiles (Vallois, 1922). Whatever the particular arrangement in cynodonts, the size of the costal plates is evidence that the M. iliocostalis dorsi was well developed and probably the strongest of the epaxial systems. The insertions on the costal plates were most likely limited to the posterior margins of the plates, which are slightly swollen, and the bulbous costal tubercles. The remainder of the dorsal surface was probably free of muscle fiber attachment because during lateral flexure this area appears to have been rather snugly covered by the next adjacent plate.

The second and third cervical ribs of monotremes possibly represent morphological derivatives from a cynodont pattern. In *Ornithorhynchus* the axis bears a flat, platelike rib (*r*, Fig. 7; cf. Lessertisseur and Saban, 1967: fig. 348) which apparently persists freely articulating throughout life. The axis rib resembles in general form the expanded proximal ends of the cervical ribs in *Thrinaxodon* (see p. 57) although distally it lacks an attenuating shaft. The third cervical rib resembles the axis rib but is smaller and synostoses with its vertebra to form a very elongate transverse process. Remaining cervical ribs, also fused, are more comparable to transverse processes typical of mammalian cervical vertebrae. The caudally directed axis rib overlaps and contacts the third cervical rib. A synovial joint appears to be developed at the point of contact. Imbrication and intercostal joints are principle features of cynodont rib specialization and the association of these features in *Ornithorhynchus* is possibly a retention rather than a parallel development. The morphology of *Tachyglossus* cervical ribs is similar except that the axis rib is also synostosed. Virchow (1929) reported that the major muscular attachments to the axial rib in *Ornithorhynchus* were the rectus capitis lateralis and the so-called spinotransversalis cervicis. The homology of the latter muscle is in doubt. Its continuity with the iliocostalis might suggest derivation from this group. Such an interpretation would be consonant with the hypothesis that cynodont rib plates were related to the iliocostalis group. However, Virchow concluded that the spinotransversalis cervicis is a specialized derivative of the longissimus, which in cynodonts probably lay immediately medial to the rib plates. Vallois (1922) claimed that in *Tachyglossus* the longissimus attaches to the cervical ribs but here also there is doubt as to the homology. The function of these ribs in monotremes should be investigated.

The Possible Functions of Cynodont Costal Plates

The association of an apparently well-developed iliocostalis muscle with costal plates must have been functional. Unfortunately the analogous condition has never evolved in any other fossil or living group, although the expanded ribs of certain modern edentates are probably comparable to a degree. Two functions of the axial skeleton which are most likely to have been related to the development of costal plates are locomotion and posture. Locomotion will be considered first.

The comparative study of Vallois (1922) shows that among living reptiles the lateral system, the iliocostalis, is relatively larger than in mammals. Moreover Vallois

established that the iliocostalis usually comprises the greater part of the reptilian epaxial musculature, the exception being that in Chelonia the epaxial system of the trunk is vestigial and undifferentiated. Obviously these facts are related to a mode of locomotion in which lateral flexure of the trunk is an important mechanism for advancing the limbs. Slijper's observation (1946: 44) that ribs act as levers which effect these movements is fundamental to understanding the basic mechanism of such locomotion. The efficiency of lateral flexure per unit of muscular contraction varies with the distance from the axis of flexure, i.e., from the vertebral column. Semispinalis fibers of the transversospinalis system, for example, have a short moment arm with respect to the vertebral axis, while fibers of the more lateral longissimus system have a relatively longer moment arm. Assuming that the contractile properties of these muscles are equal, the transversospinalis is less efficient than the longissimus in producing lateral flexure. Gans and Bock (1965) review various factors which invalidate this assumption. However the question here is one of simple mechanics, without reference to the relative efficiency of the energy (muscles) involved. The transversospinalis produces a greater degree of lateral flexure per unit of contraction, which means that it is more advantageously located, all factors being equal, to produce rapid flexing movements. The iliocostalis, the most laterally situated of epaxial musculature, occupies the most mechanically advantageous position to effect lateral flexure. In cynodonts this muscle could have been hypertrophied to generate a great amount of muscular power at a mechanically efficient position. The result, of course, would emphasize a reptilian rather than a mammalian mode of locomotion. In view of the fact that the appendicular anatomy retained so many primitive characteristics, it is perhaps not surprising that locomotory specialization should occur in the axial skeleton.

To account adequately for morphological details of the costal plates would require knowledge of the precise arrangement of the iliocostalis. Even so, the costal plate series shows a morphological gradient that could be studied functionally only in the living animal. Nevertheless a few speculative deductions may be made on the basis of osteological evidence alone.

The initial impetus for costal plate formation may have resulted from the fact that a convex flange increases the insertional area. A sharply curved posterior border unquestionably provides a longer linear surface than does the comparable length of a normal rib shaft. The costal tubercle, reflected dorsally so as not to impinge upon the adjacent longissimus, may have been an extension of this insertional area.

If a costal plate is examined on its ventral side, the ridge which represents the original rib axis, or shaft, passes near the anterior edge of the plate (Figs. 13D, 16). Therefore the bulk of costal plate expansion has taken place posteriorly. The effect has been to move the iliocostalis insertion also posteriorly (from *A* to *B*, Fig. 16). The lever arm of a posteriorly directed iliocostalis force (*F*) is the same if the muscle inserts at point *B*, as in cynodonts, or at point *A* as is the usual condition among other tetrapods, for the displacement due to plate expansion is more or less perpendicular to the lever arm.

However, there is another force generated by the iliocostalis which in certain positions of the spinal column may assist lateral flexure. This force results from the tendency for a non-linear elastic body to straighten itself during flexion. In other words, the iliocostalis tends to assume the position of the vertical dotted line in Figure 16. As

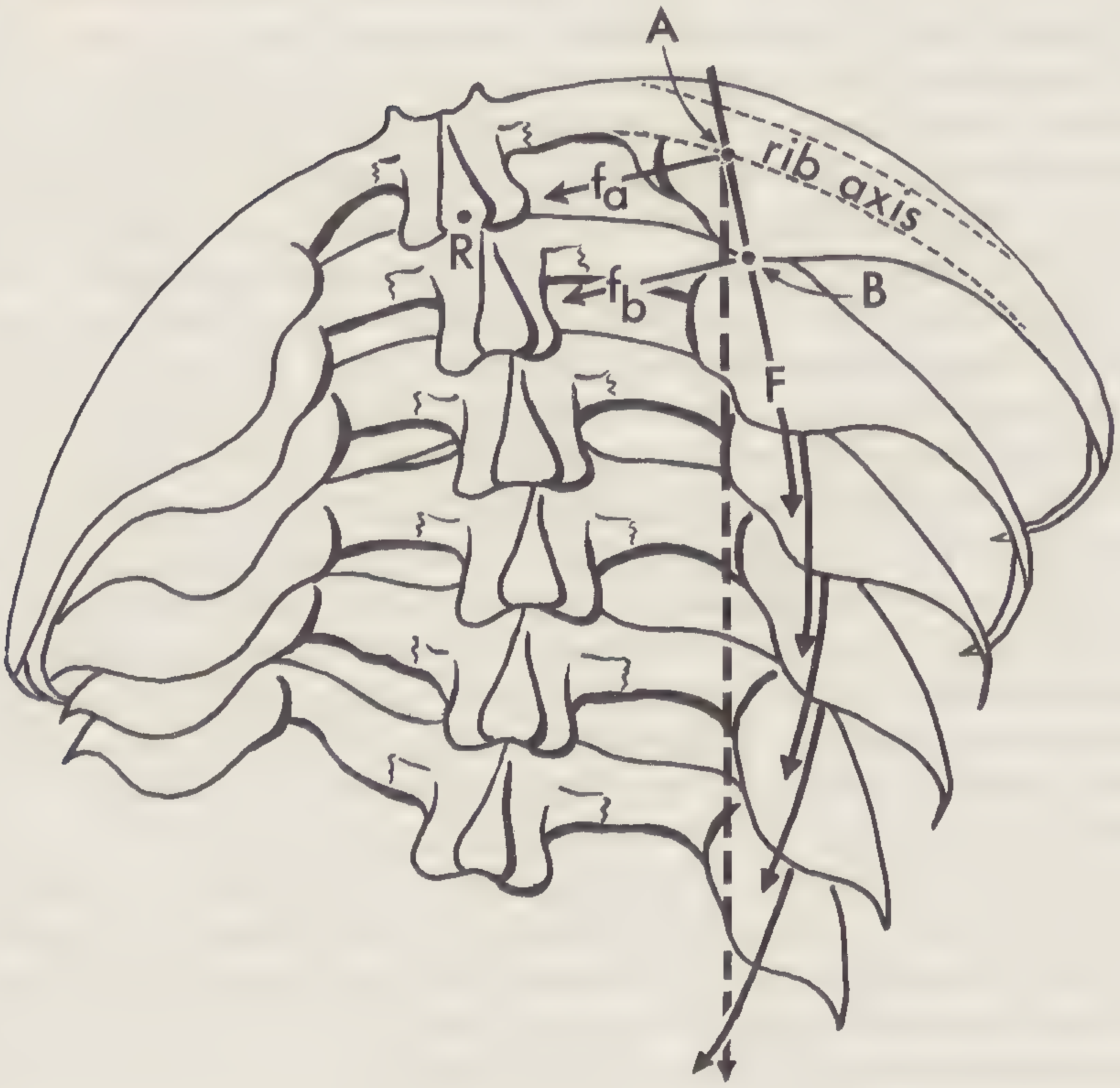

FIG. 16. Diagrammatic representation of six thoracic vertebrae and ribs of *Thrinaxodon* to illustrate the possible effect of iliocostalis force (F) applied at the edge of a costal plate (B). The iliocostalis, initially acting along an arc, tends to straighten itself to the heavy dashed line. In so doing it generates a medially directed force (f_b) at point B. The force f_b has a moment arm of AB length with respect to rotating the vertebra about point R. If the iliocostalis inserted on a normal rib at point A, the analogous force f_a would have no rotational lever arm with respect to rotation at R.

the muscle contracts, it not only increases the overlap between ribs but also exerts a medial force against its points of insertion. If the insertion (A) is directly lateral to the axis (R) about which a vertebra rotates during lateral flexure, no additional rotational effect is achieved. Instead, the force (f_a) is dissipated on the intervertebral disk and ligaments. If, however, the insertion of the muscle is displaced posteriorly (B), the medially directed force (f_b) gains a lever arm with respect to the vertebra and tends to rotate the vertebra about its axis. In cynodonts the insertion is displaced posteriorly by the caudal extension of a costal plate, with a resultant lever arm length A-B of force (f_b). Hence muscular energy is retained which otherwise would not be directed toward effecting flexure of the spinal column. The fact that costal plates form a continuous surface through imbrication ensures that these forces are utilized even at points of muscle-rib contact where there is no actual insertion.

The inherent deficiency of any hypothetical analysis that treats rib plates as muscular processes lies in the failure to account for the diversity in morphology and distribution of these plates. If a single, fundamental feature common to all rib plates is

sought, the obvious characteristic is overlap or imbrication. In simplest functional terms, costal overlap gives one vertebral segment additional support by an accessory contact with the next. The possible importance of axial strength to cynodonts may have involved certain evolutionary "experiments" in posture.

Postural differences between reptiles and mammals involve features which are either mutually exclusive, e.g., the orientation and excursion of the humerus is consistently different between the two classes, or differ in the degree to which they are employed. For example, rapidly moving crocodilians will elevate the trunk well off the ground and arch the spinal column (cf. Schaeffer, 1941b: 391; Colbert, 1948: fig. 22); this behavior approximates a mammalian posture. The critical difference, however, is that crocodilians do not sustain this posture for more than a short time and are probably physiologically incapable of doing so. Costal plates in cynodonts may have represented an "experiment" in musculoskeletal adaptation to sustain a more mammalian posture. It seems plausible, at least, that a structural adaptation for mammalian posture may have preceded or evolved concomitantly with the complex of physiological adaptations for sustained activity.

Cynodont costal plates would have provided intrinsic strength to the vertebral column, regardless of the associated musculature. The imbrication of successive ribs is a simple mechanism to ensure axial support and thus to maintain a posture in which the trunk is held off the ground. I have shown that the anteroposterior expansion of ribs among certain living edentates probably may be related to thoracolumbar stability (Jenkins, 1970b). This stability is employed in digging (*Myrmecophaga, Tamandua*) when the trunk and hind feet serve as a stable base for the powerful forelimb stroke. In the Least Anteater (*Cyclopes*) thoracolumbar rigidity is employed in arboreal locomotion; with the hind feet and prehensile tail grasping a branch, the rest of the body is stretched out to reach an adjoining branch. This maneuver is believed to be accomplished in part by virtue of the overlapping ribs. The intercostal muscles "lock" one rib against another, thus forming a trunk so rigid that it can remain in a horizontal position without support of the forefeet. Obviously the overlapping costal plates of cynodonts do not represent a parallel fossorial or arboreal specialization. But certainly the effect was analogous. Whether the increase in intrinsic vertebral column strength was a locomotory or postural adaptation, as here suggested, or due to some other habitus factor cannot be established at present.

The phylogenetic distribution of cynodont costal plates is another aspect of the problem. The earliest known cynodonts, e.g., *Leavachia*, from the *Cistecephalus* zone, apparently possessed normal, unexpanded ribs (see Jenkins, 1970a, for a possible exception to this point). By *Lystrosaurus* zone times cynodonts such as *Thrinaxodon* developed costal expansions on all presacral ribs. During the Middle Triassic, which saw the last of cynodonts in any abundance, expanded ribs are found typically in the most posterior thoracic and lumbar region. In *Cynognathus*, however, there is evidence of a slight costal expansion on the axis rib and to a lesser degree on the sixth and seventh cervical ribs. The tendency toward reduction of rib specialization is particularly well documented among South American traversodontids (Bonaparte, 1963a; Jenkins, 1970a).

Both diademodontids and cynognathids, which are quite divergent in cranial morphology and particularly in dentition, elaborate the interlocking mechanism between

the lumbar rib plates (see above, p. 73). Morphologically both the lumbar and posterior thoracic ribs appear to be very similar among representative Middle Triassic genera; the scant material available from *Cynognathus* (BMNH R.2571; UCMP 42729) and *Diademodon* (NMB 531, USNM 23352), at least, shows no significant differences. The paradox is that galesaurids, with the most extensive development of costal plates, precede Middle Triassic cynodonts in which only the posterior dorsal ribs bear the characteristic modification. If the galesaurid pattern is ancestral to the cynognathid-diademodontid pattern, then a reduction of this feature occurred, except in the lumbar series where it was further elaborated. If, on the other hand, Middle Triassic cynodonts were not derived from a galesaurid with a full complement of expanded ribs, then the question arises as to what extent are similarities due to common ancestry or parallel evolution. Were cynodont phylogeny better known, the course and perhaps the adaptive factors of costal plate evolution would be more apparent.

Whatever the evolutionary course of costal plates, certain tentative deductions may be made from their distribution and morphology among the most advanced cynodonts. In these forms costal plates are restricted to the posterior dorsal region and are absent or little developed elsewhere. Their retention and further elaboration in the "lumbar" region is perhaps indicative of their functional suitability to resist structural weakness in this area.

As a general rule the lumbar region among mammals is reinforced by several features not found elsewhere along the column. Lumbar centra are commonly the most massive of all centra. The lumbar column is further stabilized by a strong M. erector spinae, representing the fused Mm. longissimus and transversospinalis systems. The thoracolumbar aponeurosis, usually thickest in the lumbosacral region, represents a sturdy attachment for erector spinae fibers. Furthermore the lumbar column is supported by subvertebral muscles, the M. psoas major (from lumbar vertebrae to femur) and M. psoas minor (from lumbar vertebrae to ilium). All these features are attributable, at least in part, to the fact that the lumbar column must transmit the hind feet thrust forward against the inertia of a large percentage of body weight. In addition the lumbar region in many mammals is an area of significant mobility. Yet this region lacks ribs, and thus the possibility of muscular attachment thereto, which would contribute to its ability to withstand both intrinsic, i.e., weight, and extrinsic, i.e., locomotory thrust, forces. In edentates of fossorial habitus xenarthrous vertebrae occur in the lumbar and posterior thoracic region; this feature apparently contributes to lumbothoracic rigidity, or "body bracing", during fossorial activity (see Jenkins, 1970b). Another not uncommon adaptation to reinforce the lumbar region is to shorten it altogether.

In cynodonts the typical mammalian adaptations for lumbar support were apparently not developed, or at best were only incipiently developed. Lumbar centra are slightly longer and not significantly wider than anterior dorsal centra; the degree of differentiation is not greater than that found among living reptiles. For reasons given above (see pp. 83-86), cynodont epaxial musculature is believed to have retained a primitive tripartite arrangement and probably did not develop a true M. erector spinae and thick thoracolumbar aponeurosis as in mammals. Furthermore, it is very likely that cynodonts had not yet developed a mammalian arrangement of psoas muscles. Romer (1922b: Pl. XLV) reconstructed the homologues of these muscles in

Moschops as arising from the pubis, which is the primitive, reptilian origin. For reasons given below (see p. 181) it appears that this muscle mass in cyndonts was similarly disposed. Dorsal migration to a mammalian position had not yet occurred. Thus an M. psoas minor could not have been present to aid in fixation of the lumbar series.

The absence of lumbar specializations typically associated with a mammalian posture does not constitute proof that costal plates were a primitive adaptive substitute. However, if advanced cynodonts were making certain physiological advances toward mammalian behavior, then it is reasonable to expect that the musculoskeletal system should have responded to the stresses induced by such activity. Certainly the lumbar region, together with the pelvis, underwent profound changes in the therapsid-mammalian transition in response to a basic functional reorientation; costal plates may well represent an early manifestation of the selective processes which eventually formed the mammalian pattern.

PART TWO. APPENDICULAR SKELETON: PECTORAL GIRDLE AND FORELIMB

1. PECTORAL GIRDLE

Scapulocoracoid (Figs. 17–21)

MATERIAL. The cynodont shoulder girdle is composed of a scapula, coracoid, procoracoid, clavicle and interclavicle. A cleithrum is not present. In no cynodont is a complete, associated shoulder girdle known. However numerous specimens of *Thrinaxodon* (AMMM 5265; NMB C.392; SAM K.1395; and USNM 22812, among others) provide an adequate picture of the morphology of separate elements. In addition incomplete scapulocoracoids are known in *Cynognathus* (BMNH R.2571; UCMP 42729). Broom (1909) gave a brief description of a *Cynognathus* scapulocoracoid, clavicle and interclavicle, but the specimen is not figured and cannot be located. Brink (1955) described and figured a scapulocoracoid (DMSW 224) which he identified as *Diademodon laticeps*; however for reasons already made clear (see footnote, p. 13) both generic and trivial identifications are in doubt. Two collections (BPI 1675; NMB C.2698, C.2700, C.2711) in which disassociated remains of *Cynognathus* and *Diademodon* have been intermixed show that the shoulder girdle elements of these genera are extremely similar and cannot be distinguished, presently at least, without diagnostic cranial material. Indeed the morphology of shoulder girdle elements of *Thrinaxodon*, *Cynognathus* and *Diademodon* is so uniform that a single description suffices; persistent minor variations are mostly due to differences in ossification. The girdles of other cynodonts are either unknown or are too fragmentary to permit reliable comparison.

The scapula of *Galesaurus* is known from a very incomplete specimen (SAM K.1119) and another specimen (UMC R.2722) which is rather complete but is not certainly identified as belonging to this genus.

The poorly preserved scapulocoracoid of *Glochinodontoides* (TM 83) described by Haughton (1924) is only tentative confirmation of its similarity to the scapulocoracoid of other cynodonts.

A partially prepared specimen of *Leavachia* sp. (BPI 374) and the type of *Leavachia duvenhagei* (RC 92, described by Broom, 1948: 618–627 and again figured by Brink and Kitching, 1953a: 315) indicate the procynosuchid girdle is essentially the same as that of any other family of South African cynodont. Neither specimen is com-

pletely prepared, however. Brink and Kitching's figs. 1 and 2, made after further preparation has been undertaken on the type specimen, shows that Broom's fig. 40 is a largely hypothetical reconstruction of the coracoids. Without complete preparation of existing specimens or the recovery of new material the pectoral morphology of *Leavachia* must remain somewhat in doubt.

Owen (1876: 21) briefly described the coracoids in *Cynochampsa laniarius*, a genus considered questionably synonomous with *Diademodon* by Watson and Romer (1956: 65). These specimens, numbered S.A. 42 and S.A. 43, were presumably part of the British Museum (N.H.) collection, but could not be located for study.

MORPHOLOGY. The scapula is markedly bowed laterally and bears a high, narrow blade, the vertebral border of which is anteroposteriorly expanded. However the greatest surface area is found across the middle of the blade where the sharp lateral flexure of the cranial and caudal borders forms a narrow but deep fossa for the M. supracoracoideus (*f spc*, Figs. 17A, 18A). This muscle, generally considered to be the homologue of the mammalian spinati, was probably most strongly developed where the fossa is deepest, i.e., across the middle of the scapular blade. Therefore it is possible that its dorsal migration was as yet incomplete (cf. Gregory and Camp, 1918: 511; Romer, 1922b: 532ff.; Jouffroy and Lessertisseur, 1967: fig. 10). The supracoracoideus fossa does not extend ventrally to the glenoid but terminates as a narrow, open groove well up on the blade (*gr*, Fig. 18A); from this groove the muscle, perhaps in part or wholly tendinous, ran to its insertion on the greater tuberosity. The caudal border of the scapula extends to the edge of the glenoid as a clearly defined crest, although at the scapular base it is merely a low ridge and not a free flange of bone as along the cranial border. The flange of the cranial border continues to the scapular-procoracoid contact as a thin sheet of bone. Ventrally, however, the cranial border is everted so that it is directed anteriorly instead of laterally (Figs. 17C, 18C). This part of the scapula appears to have been very thin and in only a few known specimens is it preserved in nearly complete condition. Apparently the clavicle articulated with the scapula here, but this articulation is not well preserved in any known specimen.

An acromial process appears not to have been developed in *Thrinaxodon*, for in excellently preserved specimens the everted edge is extremely thin and apparently complete. In the best preserved specimens a localized thickening occurs on the dorsal half of the everted edge and this may represent the point of acromioclavicular articulation (*?acr*, Fig. 18C). In *Galesaurus* Broom (1932b: 279) claimed that the acromion "is merely a fold on the anterior edge of the bone." In *Cynognathus crateronotus* (BMNH R.2571) there is a robust acromial tuberosity protruding anteriorly from the dorsal half of the edge (Seeley, 1895b: 93; see also Broom, 1909). A similar acromion apparently occurs in *Diademodon* (Brink, 1955: 28), although in most known specimens (*acr*, Fig. 17C) it is invariably damaged or lost.

An anteroventral division of the M. supracoracoideus probably originated in the two shallow concavities along the adjacent anterior borders of the scapula and procoracoid (*spc*, Fig. 19F). Such an arrangement might represent an early stage in the differentiation of the mammalian infra- and supraspinatus muscles (for a brief review of various opinions as to the reptilian homologues of the Mm. spinati, see Romer, 1922b: 532 ff. and Howell, 1937b). However it is improbable that the anteroventral

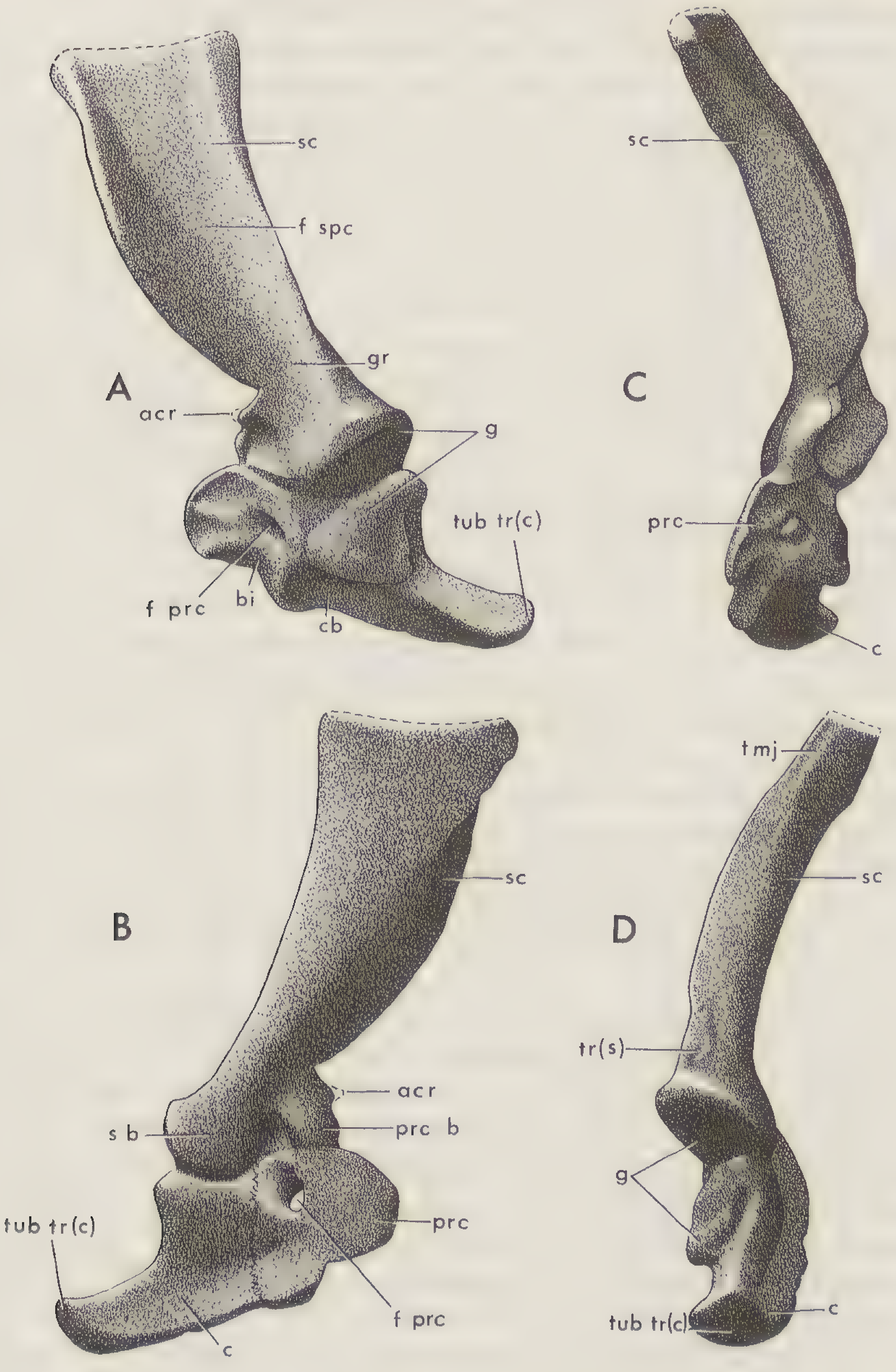

FIG. 17. Left scapulocoracoid of cf. ?*Cynognathus* (?*Diademodon*), NMB C. 2711. A, lateral; B, medial; C, anterior; D, posterior views. The acromion has been broken off and is restored (dashed line) in A and B. The vertebral border of the scapula has likewise been restored; in life the scapula was probably extended by a cartilaginous suprascapula, not shown. X0.4. Abbreviations: *acr*, acromion process; *bi*, fossa for origin of biceps muscle; *c*, coracoid; *cb*, fossa for origin of coracobrachialis muscle; *f prc*, procoracoid foramen; *f spc*, supracoracoid fossa homologous with mammalian infraspinatus fossa; *g*, glenoid; *gr*, groove marking ventral termination of supracoracoid fossa; *prc*, procoracoid; *prc b*, procoracoid buttress; *s b*, supraglenoid buttress; *sc*, scapula; *t mj*, groove presumed to represent teres major origin; *tr (s)*, shallow groove presumed to represent scapular head of triceps origin; *tub tr (c)*, tuberosity for origin of coracoid head of triceps.

division of the supracoracoideus had any fibers running beneath the clavicle to the medial surface of the scapula, thus functioning as a true supraspinatus; the flange extends so far anteriorly that fibers passing to the medial surface would turn an angle of at least 180°. On this basis Romer (1922b: 535) argued against the possibility of a mammalian supraspinatus in *Cynognathus* and the argument is equally valid for all other cynodonts in which the scapulocoracoid is known. Yet Sukhanov (1961) found that in the agamid *Phrynocephalus mystaceus* a supracoracoideus fascicle passes beneath the clavicle and around the anterior border of the scapula to attach to the medial scapular surface. In reaching this surface the fascicle must turn an angle of approximately 180°. The muscular arrangement that Romer believed to be theoretically improbable is in fact possible. Nevertheless the relatively large size of the cynodont procoracoid and its close apposition to the clavicle appears to have blocked any supracoracoideus fibers from passing beneath the clavicle to the medial scapular surface (see frontispiece). To open a route for supracoracoideus migration either the acromioclavicular articulation must displace relatively dorsad, as in *P. mystaceus*, or the procoracoid must be reduced. Coracoid reduction seems to have been a principal factor in the evolution of the mammalian supraspinatus and may have initially involved the development of fenestrae; the cynodont coracoid is already sculptured by fossae. An analogy may be drawn with the fenestrae in the scapulocoracoid of *Iguana* that encircle the origins of the Mm. supracoracoideus, biceps and scapulo-humeralis anterior (Fig. 19E).

Monotreme shoulder musculature has undoubtably specialized to some degree and should not be interpreted a priori as a "prototherian" prototype. This point is well exemplified with reference to the spinati. Howell (1937a: 203–204), in a classic comparative study, investigated the possibility of an infra- and supraspinatus in monotremes and concluded that precise homologues could not be determined. He wrote that:

> It is extremely likely that in the broad sense these muscles [i.e., the coracohumeralis intermedius and profundus, which, in Fig. 19G, are indicated simply as supracoracoideus] of monotremes represent mm. supraspinatus, infraspinatus, and possibly the anterior part of subscapularis of placentals, but it cannot be stated without reservation that the deepest division of the former sort of mammal represents any particular one of the three muscles of the latter sort. . . . In this connection it must be remembered that the monotremes are very much specialized, and that in them suprascapular musculature, although definitely suggested, apparently has been arrested far short of the conditions indicated in Permian dicynodonts, or even some of the cotylosaurs. Accordingly the precise arrangement of the deeper coracoid musculature that finally gave rise to true suprascapular musculature may have been quite different from that now encountered in monotremes.

Even on the assumption that monotremes retain a semblance of a therapsid muscular arrangement, the major obstacle to interpreting cynodont shoulder musculature on the basis of the monotreme pattern is the dissimilarity of cynodont and monotreme scapulae. Details of this dissimilarity will be discussed with reference to individual muscles.

The caudal border of the cynodont scapular blade extends from the vertebral border to the upper rim of the glenoid and represents a division between medial and lat-

eral aspects of the scapular blade. The caudal border is here interpreted to represent a division between the area of attachment of the subcoracoscapularis and scapular triceps muscles medially and the supracoracoideus and teres muscles laterally.

In larger cynodonts, especially those represented in the BPI 1675 collection, a vertical, linear depression occurs on the lateral aspect of the scapular blade immediately above the glenoid rim and adjacent to the caudal border. This feature, facing posterolaterally, may represent the origin of a teres minor (*t mn*, Fig. 19F). The scar is not found in all cynodont scapulae and is invariably absent in smaller species in which ossification is generally less complete. Romer (1922b: 532) believed the M. scapulo-humeralis anterior of reptiles to be the homologue of the mammalian teres minor. However Howell (1937b), followed recently by Jouffroy and Lessertisseur (1967), argued convincingly that the teres minor is a derivative of the reptilian M. dorsalis scapulae and therefore primitively associated with the deltoid. Cynodonts offer no evidence for either of these alternatives. Whether a derivative of the scapulo-humeralis anterior or the deltoid, the mammalian teres minor must have undergone posterior migration to reach its characteristic position along the caudal border of the scapula.

The teres minor as here reconstructed in cynodonts is positioned essentially as a mammalian teres minor. Gregory and Camp (1918: 471) gave a similar reconstruction for this muscle in *Cynognathus* although they illustrated the origin as being slightly more anterior. The present interpretation aside, the question remains whether the teres minor differentiated before or after the scapular invasion of the supracoracoideus. The position of the large teres minor and relatively undifferentiated supracoracoideus in monotremes (as identified by Howell, 1937b, and Jouffroy and Lessertisseur, 1967) is suggestive of the former. This possibility is based on the assumption that the basic arrangement of monotreme shoulder musculature is primitive for mammals—an assumption which cannot be supported by direct evidence at present. The teres minor of monotremes occupies a position analogous to that of the groove on cynodont scapulae which I have interpreted as the supracoracoideus origin (see above). Thus the cynodont scapular groove may represent a teres minor rather than a supracoracoideus origin.

In cynodonts the scapular head of the triceps took origin from the medial surface of the scapula adjacent to the caudal border. This surface faces posteriorly and in many specimens bears a shallow groove which presumably marks the origin [*tr*(*s*), Figs. 18D, 19F]. The groove is variably developed and in the larger cynodonts it is often scarcely discernible [*tr*(*s*), Fig. 17D]. In the type of *Cynognathus crateronotus* (BMNH R.2571) however, the origin of the scapular triceps is marked by a rugose tuberosity (see Seeley, 1895b: fig. 10).

The teres major, as reconstructed by Gregory and Camp (1918: 471) and Romer (1922b: Pl. XXXIII) in *Cynognathus*, takes origin from the caudal angle of the scapula. In all cynodonts the bone of the caudal (and cranial) angle is thicker than elsewhere on the scapular blade. In *Cynognathus* and *Diademodon* a groove on the thickened caudal edge below the angle is undoubtedly associated with the origin of the teres major (*t mj*, Figs. 17D, 19F). The medial wall of this groove extends posteriorly and serves as the origin for the serratus anterior musculature (Fig. 19F). A groove is not present in *Thrinaxodon* but the bone of the caudal angle is thickened; a

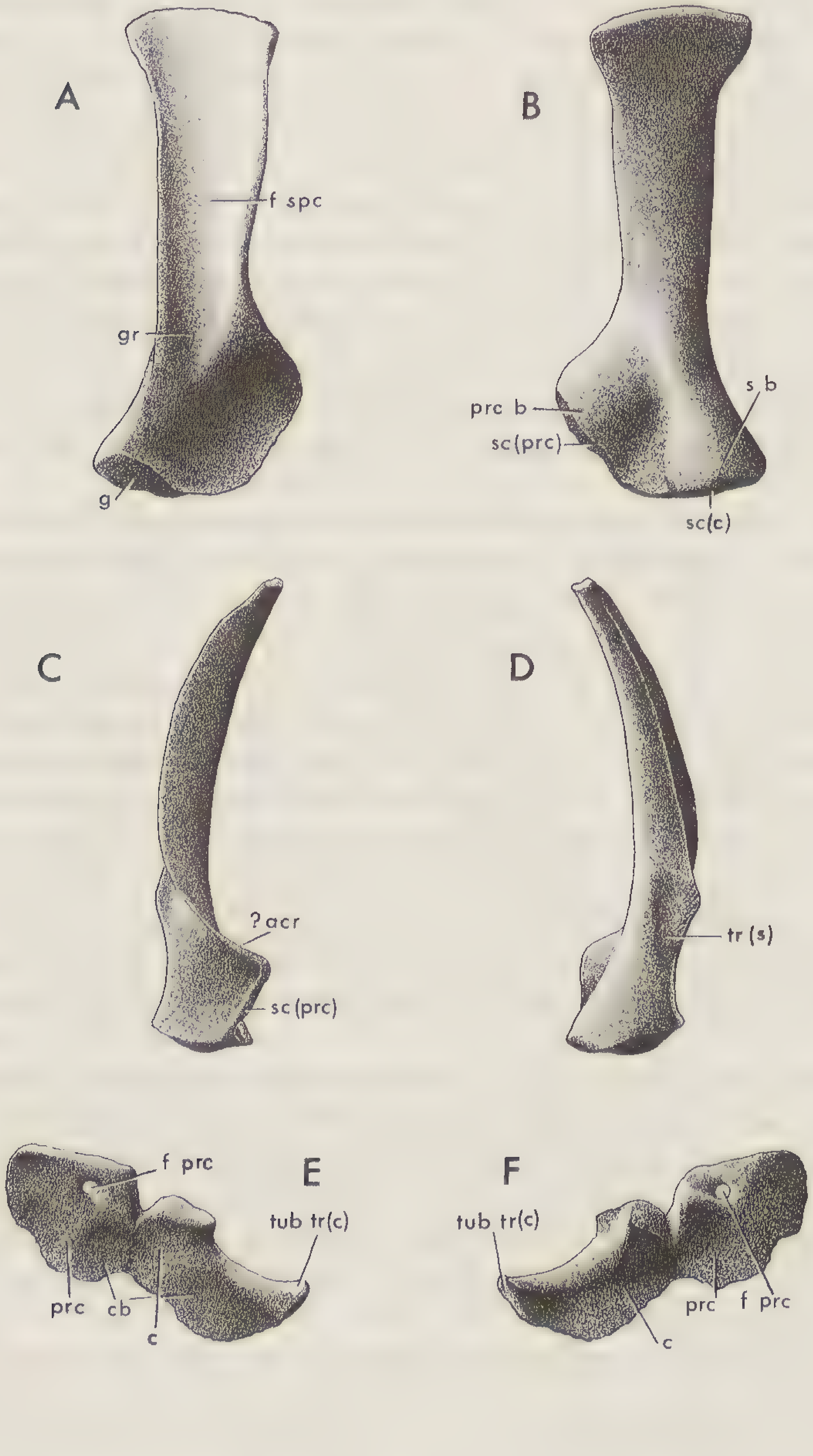

FIG. 18. The scapulocoracoid of *Thrinaxodon*, SAM K. 1395. A, lateral; B, medial; C, anterior; D, posterior views of a right scapula. E, lateral; F, medial views of left procoracoid-coracoid plate which is incomplete along the ventral margin. X1.75. Abbreviations as in FIG. 17 except: *sc (c)*, scapular articular surface for the coracoid; *sc (prc)*, scapular articular surface for the procoracoid.

groove may have been developed on the unossified suprascapula which in large cynodonts permitted a dorsal extension of the groove.

With the exception of the muscle scars for the teres major and triceps the medial surface of the scapula is a smoothly curving, featureless plate which is readily described morphologically but which is difficult to interpret in terms of subscapular musculature. In medial view the scapular blade is concave dorsoventrally, except for a small area ventral to the vertebral border which is usually flat but which may be very shallowly concave (Figs. 17B, 18B). Anteroposteriorly the blade is convex, again with the exception of the area below the vertebral border.

The medial surface of the scapular blade may be roughly divided into cranial and caudal parts along the line of sharpest anteroposterior curvature. This line passes obliquely down the blade from the cranial angle posteroventrally to the joint between the supraglenoid buttress (*s b*) and the coracoid (*c*, Fig. 17B). The caudal part posterior to this line may be interpreted as the locus of origin of the Mm. subcoracoscapularis, serrati and levator scapulae (*sbcsc*, *ser* and *lev scap*, Fig. 20F); the cranial part represents the origin of the deltoid homologue, the dorsoscapularis (along the cranial border; *dsc*, Fig. 19F), and the insertion of part of the trapezius and levator scapulae musculature (*tzs*, *lev scap*, Fig. 20F).

Evidence for a reconstruction of cynodont subscapular musculature is derived from subscapular musculature in living reptiles and the inferred arrangement in other fossil forms. In *Sphenodon* and lizards the entire subscapular muscle mass, commonly referred to as the M. subcoracoscapularis, runs from an origin on the medial surface of the scapula and coracoid to the proximal internal angle of the humerus (*sbcsc*, Fig. 20D, E). This muscle is incompletely divided into posterodorsal and anteroventral divisions by a sterno-scapular ligament. The dorsal part is thought to be homologous with the M. subscapularis of mammals and in addition has fibers not represented in mammals which gain access to the lateral face of the scapula as the M. scapulohumeralis posterior (Romer, 1922b: 530–532; *sch p*, Fig. 19D, E). Anteroventral to the sterno-scapular ligament is the M. subcoracoideus; the question of its presence in cynodonts is discussed later with reference to the coracoid. Romer (1922b: 530) concluded that in primitive reptiles and pelycosaurs the entire subcoracoscapularis was confined to the dorsal half of the medial scapular blade and was probably not differentiated as in living reptiles. The origin is clearly defined as a shallow, triangular concavity, its "base" lying along the vertebral border and its "apex" pointing posteroventrally toward the glenoid (Fig. 20B, C). From the "apex" the subcoracoscapularis muscle passed posterolaterally around the caudal border of the scapula, where a broad trough is developed to facilitate its passage. The caudal part of the medial scapular surface in cynodonts is not greatly changed from this condition (Fig. 20F). The most significant differences are that the subcoracoscapularis origin extends nearly to the base of the scapula, as in mammals, and that the inserting end of the muscle does not circumvent the caudal border of blade as it did primitively, and still commonly does in living reptiles. Instead in cynodonts the insertion into the lesser tuberosity probably was reached by subcoraco-scapularis fibers emerging from the medial side of the scapula along the posterodorsal edge of the glenoid. This condition approximates that of mammals in which subscapularis fibers pass ventrally along the medial side of the glenoid capsule to reach the lesser tuberosity.

The cranial part of the medial scapular surface is a broad flange which faces primarily anteriorly and attenuates dorsally and ventrally (Figs. 17C, 18C). The cranial border in fact extends farther laterally than does the caudal border. It is improbable that the breadth of the cranial sector is in response to the requirements of the M. supracoracoideus alone (on the lateral face), but in view of the lack of muscle scars on this part of the medial surface it is impossible to reconstruct confidently the muscular arrangement. Levator scapulae and serratus musculature undoubtedly took origin from the area below the vertebral border (*lev scap*, *ser*, Fig. 20F), characterized in cynodonts by a lack of curvature in the blade and in some cases by a slight depression on the medial surface. Such a position is analogous to the origins of these muscles in living tetrapods as well as the inferred conditions in other fossil forms. The cranial section of the medial surface probably afforded insertional area for deep layers of the levator scapulae and possibly trapezius as well. Gregory and Camp (1918: Pl. XL) gave a reconstruction of the musculature on the medial side of the scapula of *Cynognathus*; this reconstruction, which delineates discrete areas for trapezius, omotrachelian and levator scapulae profundus musculature, is based primarily on an assumed analogy with *Ornithorhynchus*. However the medial side of the monotreme scapula is quite flat, as opposed to that in cynodonts which has a complex curvature. Furthermore the caudal half of the scapula is both shaped and oriented differently in monotremes. This difference is due in part to the posterior displacement of the caudal angle from which the teres major takes origin (a specialization common in fossorial forms); another peculiarity is the extensive invasion of the subscapularis (*sbsc*, Fig. 19G) onto the lateral surface (a development paralleled among reptiles; *sbcsc*, Fig. 19D, E). Neither of these features can be attributed to cynodonts. Monotremes offer no certain guide to the arrangement of cynodont subscapular musculature.

The base of the cynodont scapula bears a hemicircular articular facet, which is the scapular (dorsal) half of the glenoid (*g*, Fig. 18A), and two surfaces for articulation with the coracoids [*sc*(*prc*), *sc*(*c*), Fig. 18B, C]. The rough texture of all three bone surfaces testifies to an extensive cartilaginous covering during life. In old individuals the joint between the scapula and coracoids may synostose (Fig. 17), but in most specimens the cartilaginous connection resulted in postmortem disarticulation.

The scapular contact with the coracoids is buttressed by two rod-like processes, one for each coracoid, on the medial aspect of the scapular base (*s b*, *prc b*, Figs. 17B, 18B). The posterior or supraglenoid buttress, the larger of the two, is incompletely separated from the anterior or procoracoid buttress by a sulcus which leads into the procoracoid foramen below. This sulcus probably accommodated the nerve on its course to the foramen. The sutural surface of the anterior buttress is narrow, flat, and faces anteroventrally and somewhat medially [*sc*(*prc*), Fig. 18C]. It contacts a similar surface along the dorsal margin of the procoracoid. The sutural surface of the posterior buttress is slightly convex and wider than that of the anterior buttress. The separation between the surface on the posterior buttress for the procoracoid and the glenoid surface is marked by a difference in orientation, but the change is gradual.

The scapular surface of the glenoid faces posterolaterally as well as ventrally. The upper lip of the glenoid is sharply defined and the glenoidal surface below it is very slightly convex (Fig. 21). Otherwise the scapular half of the glenoid is rather flat; commonly there is a broad, shallow concavity situated at the facet center and the an-

terolateral corner of the facet faces laterally (Fig. 21). The margin of the coracoid (or lower) half of the glenoid is not as symmetrical in outline as the upper half. Compared with the hemicircular plan of the scapular half, the outline of the coracoid half of the glenoid is approximately triangular. The surface faces posterolaterally and slightly dorsally. Laterally the facet margin is gently convex and long; posteromedially the facet margin is straight and short, being terminated by a slight tuberosity (*tub*, Fig. 21) before reaching the scapular-coracoid contact. The facet surface is broadly convex, flattens gradually to an even slope near the lateral margin, and bears a distinct recess (*rec*, Fig. 21) adjacent to the posteromedial margin. Seeley (1895b: 91), Watson (1917a: 25) and Brink (1955: 29) claimed that the procoracoid was excluded from the glenoid but in fact its posterodorsal corner forms a small segment of the lateral glenoidal lip between the coracoid and scapula.

The coracoid and procoracoid are invariably synostosed along a serrate suture which is usually more clearly preserved on the medial side (Figs. 17B, 18E, 22A, B). The coracoid is approximately triangular in outline. The expanded, robust anterodorsal edge [*c(sc)*, Fig. 22A] contacts the supraglenoid buttress above and acts to reinforce the coracoid part of the glenoid. The posterodorsal edge of the coracoid is a flat, wide shelf; the ventral edge is narrow and slightly convex. Both edges terminate posteriorly in a swollen tuberosity for the coracoid head of the triceps [*tub tr(c)*, Figs. 17A, B, D, 18E, F, 22]. Romer (1922b: 538) believed that this head was absent in therapsids because of the "reduced condition" of the coracoid; however his figure (Pl. XXXIII) of *Cynognathus* appears to be based on the type of *C. crateronotus* Seeley 1895 (BMNH R.2571) in which the posterior half of the coracoid is broken off. Gregory and Camp (1918: Pl. XL) and McKenna (1961: fig. 6) also figured the same specimen; the former authors placed the origins of the coracobrachialis and biceps on the broken edge of the coracoid, giving no indication of the probable disposition of the triceps' coracoid head. Broom (1909: 284), comparing the type of *Cynognathus* with another "imperfect" specimen, also concluded that the coracoid was "singularly short, and not more than 10 mm. is missing . . . in the type specimen." In fact the cynodont coracoid has a long posterior process, a primitive feature which monotremes retain. However in monotremes (see Westling, 1889 and Howell, 1937a) the coracobrachialis and a biceps head attach to the coracoid process; the possibility that this was also the condition in cynodonts is discussed below (see p. 154).

The lateral margin of the dorsal coracoid shelf is sharply delineated by the undercut surface of the coracoid. The medial margin is a gradual transition from the dorsal shelf to the medial surface, especially adjacent to the coracoid tuberosity where the surfaces are smoothly confluent. In the living animal the dorsal shelf is interpreted as facing dorsolaterally, thus permitting a muscle originating from the medial surface to pass laterally to an insertion on the lesser tuberosity of the humerus. The relations of the M. subcoracoideus in *Sphenodon* and lizards (Fig. 20D, E) are analogous to this inferred condition in the cynodonts and it seems reasonable to believe, contrary to Romer (1922b: 531–532), that cynodonts possessed subcoracoid musculature. Romer rejected the possibility that *Cynognathus* possessed an M. subcoracoideus because there is "no evidence of a separation of the subcoraco-scapularis into two parts" (ibid.). This interpretation is based on the apparently "reduced" condition of the coracoid, which, as figured by Romer, is incomplete, and Romer's contention that the muscle

A
B
C
D
E
F
G
ser
dsc
supsc
sbcsc
tr(s)
tr(c)
scha
spc
cb & bi
scha & spc
p
lev scap
clm & trp
schp
cbb
trp
sbc
t mj
t mn
tzs
dlt
sbsc
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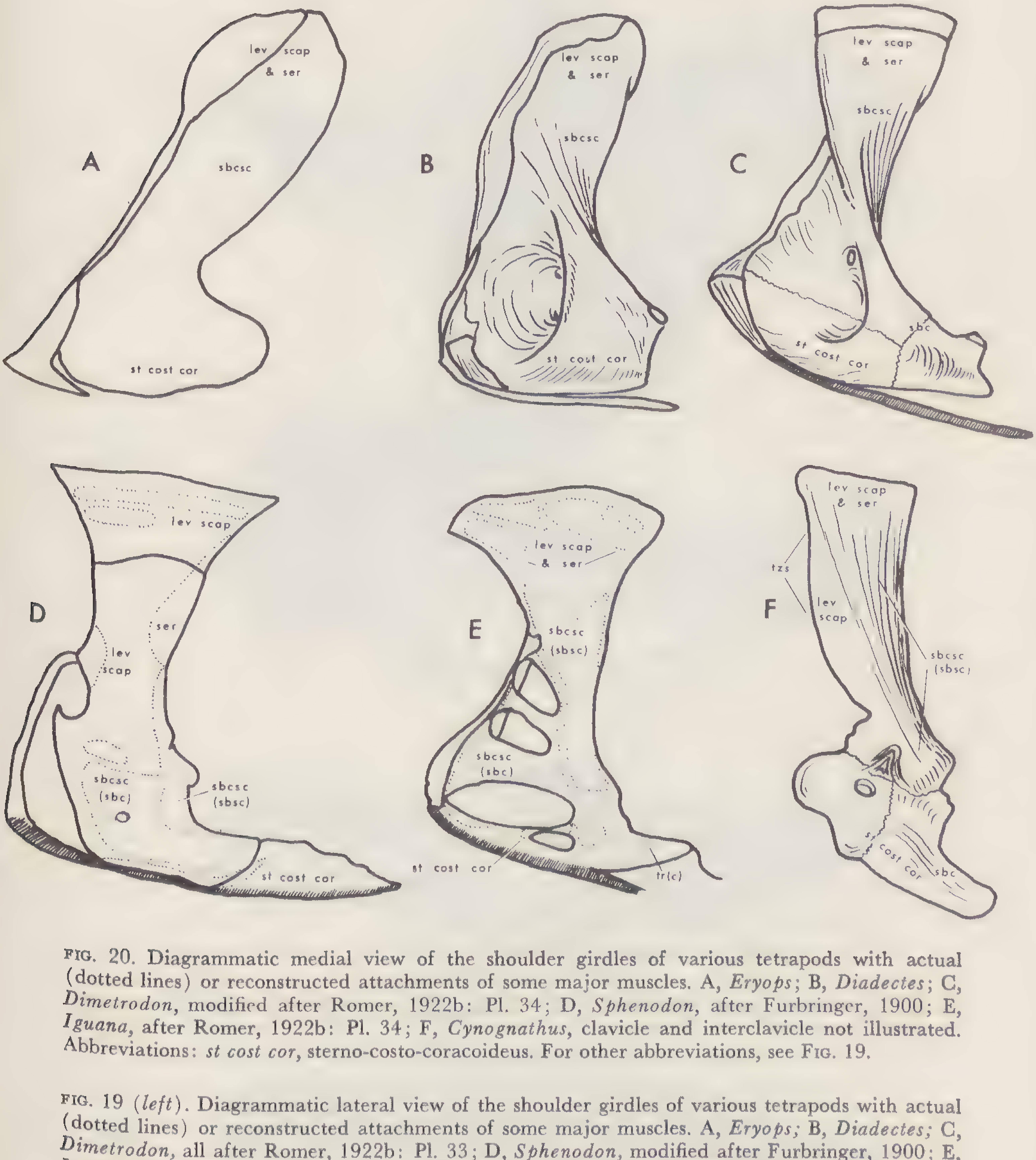

FIG. 20. Diagrammatic medial view of the shoulder girdles of various tetrapods with actual (dotted lines) or reconstructed attachments of some major muscles. A, *Eryops*; B, *Diadectes*; C, *Dimetrodon*, modified after Romer, 1922b: Pl. 34; D, *Sphenodon*, after Furbringer, 1900; E, *Iguana*, after Romer, 1922b: Pl. 34; F, *Cynognathus*, clavicle and interclavicle not illustrated. Abbreviations: *st cost cor*, sterno-costo-coracoideus. For other abbreviations, see FIG. 19.

FIG. 19 (*left*). Diagrammatic lateral view of the shoulder girdles of various tetrapods with actual (dotted lines) or reconstructed attachments of some major muscles. A, *Eryops;* B, *Diadectes;* C, *Dimetrodon*, all after Romer, 1922b: Pl. 33; D, *Sphenodon*, modified after Furbringer, 1900; E, *Iguana*, after Romer, 1922b: Pl. 33; F, *Cynognathus*, clavicle and interclavicle not illustrated; G, *Tachyglossus*, after Westling, 1889: Pl. 2, and Howell, 1937a. Not to scale. Abbreviations: *bi*, biceps; *cb*, coracobrachialis; *cbb*, short head of coracobrachialis; *cbl*, long head of coracobrachialis; *clm*, cleidomastoideus; *dlt*, deltoid; *dsc*, dorsoscapularis; *isp*, infraspinatus; *lev scap*, levator scapulae; *p*, pectoralis; *psch*, proscapulohumeralis (see Howell, 1937a); *sbc*, subcoracoideus; *sbcsc*, subcoracoscapularis; *sbsc*, subscapularis; *scha*, scapulohumeralis anterior; *schp*, scapulohumeralis posterior; *ser*, serratus; *spc*, supracoracoideus; *supsc*, suprascapular cartilage; *t mj*, teres major; *t mn*, teres minor; *tr (c)*, coracoid head of the triceps; *tr (s)*, scapular head of the triceps; *trp*, trapezius; *tzs*, trapezius.

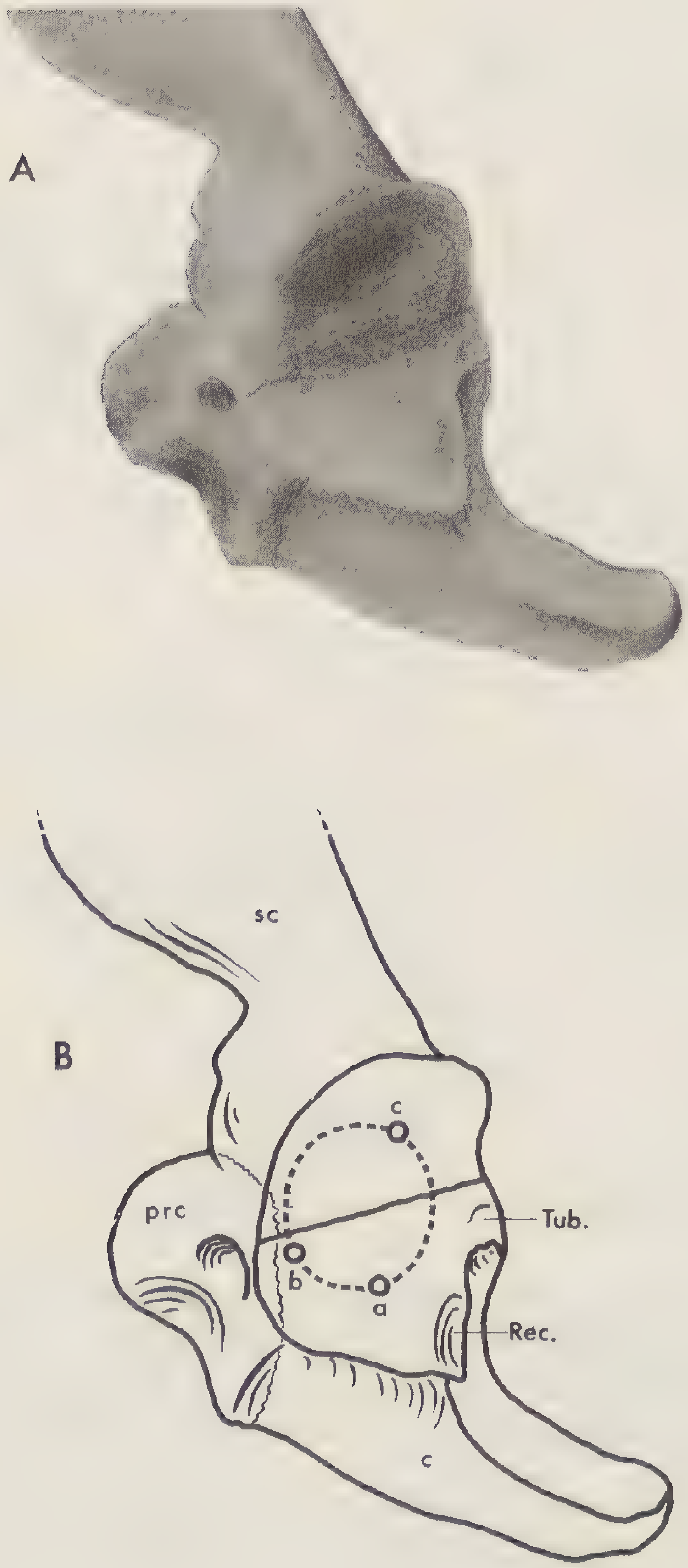

FIG. 21. A, sketch of the glenoid in a large cynodont, cf. ?*Cynognathus* (?*Diademodon*), NMB C.2711, in lateral view. B, in the line drawing of the same specimen, the dotted line represents the proposed course of a point on or near the center of the humeral head during locomotion: *a*, beginning of protractive phase; *b*, completion of protractive phase and beginning of propulsive movement; *c*, completion of propulsive movement. See text for details. Approx. X3/5. Abbreviations as in FIG. 17 except: *Rec*, recess; *Tub*, tubercle on coracoid half of the glenoid.

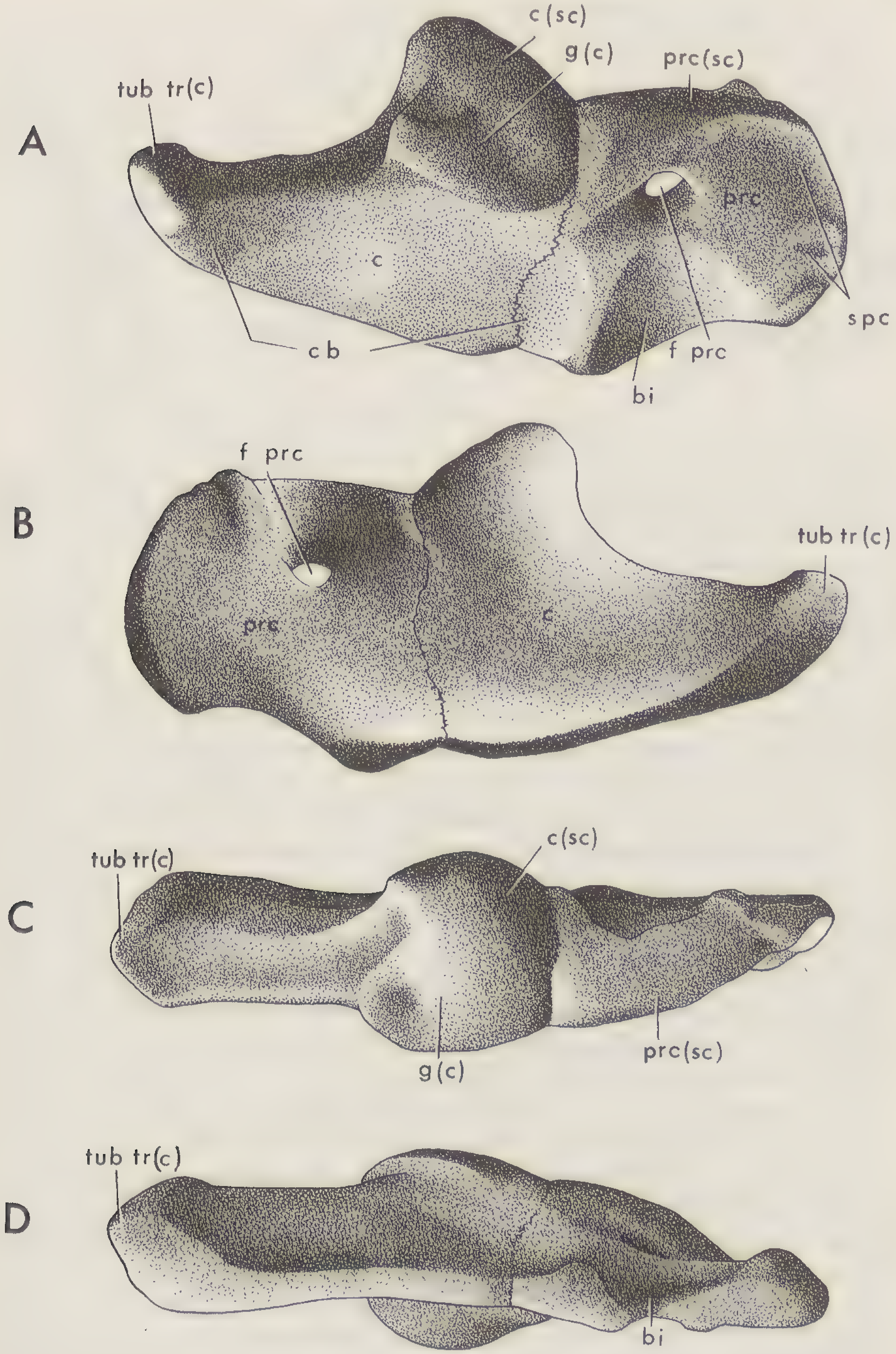

FIG. 22. The right coracoid and procoracoid of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, in A, lateral; B, medial; C, dorsal; D, ventral views. X1. Abbreviations as in FIG. 17 except: *c* (*sc*), coracoid articular surface for the scapula; *g* (*c*), coracoid part of glenoid fossa; *prc* (*sc*), procoracoid articular surface for scapula; *spc*, fossa for supracoracoideus muscle.

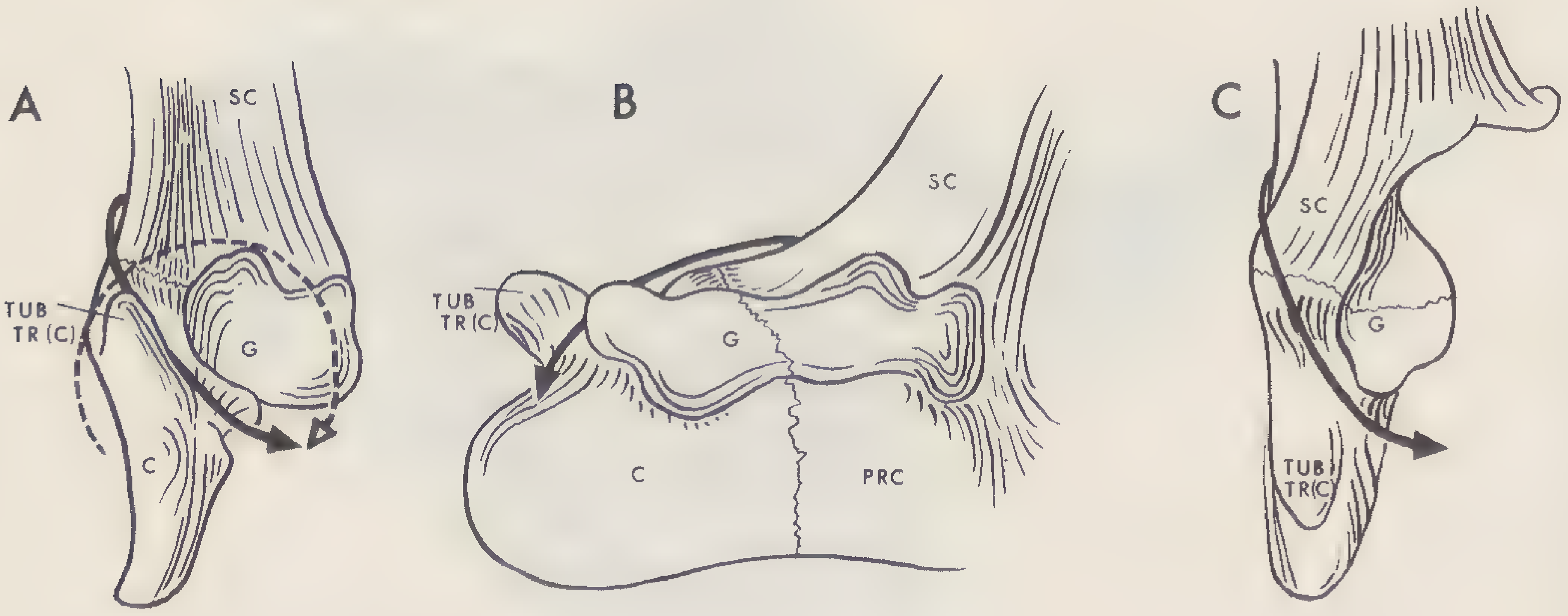

FIG. 23. Diagrammatic sketch of the glenoid region of *Dimetrodon* to show the probable course of the subcoracoideus muscle (black arrow). A, posterior; B, lateral; C, dorsal views. Romer (1922b) rejected Watson's (1917a) reconstruction of subcoracoid musculature (dotted line) on the basis that it would turn too great an angle (270°). Abbreviations as in FIG. 17.

was also absent in pelycosaurs. Romer correctly considered that a subcoracoideus origin from a fossa on the medial coracoid-procoracoid surface as proposed by Watson (1917a: 12) would require the fibers to turn an angle of approximately 270° (*dashed line*, Fig. 23A). Watson's reconstruction therefore seems improbable, but the possibility of a subcoracoideus cannot be eliminated on that account alone and the following alternative is proposed. In *Dimetrodon* as well as in most pelycosaurs, there is a distinct, broad groove in the dorsal rim of the scapulocoracoid between the tuberosity for the triceps' coracoid head and the posterodorsal rim of the glenoid (Figs. 23, 38; also see Romer and Price, 1940: 121–123). Medial to the dorsal rim of the glenoid, the sutural contact between the scapula and coracoid is swollen (Fig. 23C). This swollen rim creates a more gradual transitional surface from lateral to medial side than would be permitted by a narrower edge. Subcoracoid musculature, directed posterolaterally, could have taken origin from this swollen area as well as the adjoining medial surface; it could have reached the lesser tuberosity via the groove between the glenoid and the tuberosity for the coracoid head of the triceps without turning an angle of much more than 45°. The symmetrical and pulley-like shape of this groove is evidence of the passage of its tendon. Possibly the presence of a ligament over the groove served to restrict the course of the inserting end of the muscle. Thus reconstructed the M. subcoracoideus in pelycosaurs cannot have been a muscle of great power. The groove in cynodonts is widened to an elongate shelf, perhaps indicative of a relatively larger muscle.

In cynodonts the relationship between the tuberosity for the triceps' coracoid head and the glenoid is completely altered from the pelycosaurian condition. The tuberosity is displaced from its primitive location, posteromedial to the glenoid and at the same approximate level, to a position posteroventral to the glenoid and at a relatively much greater distance from it [*tr(c)*, Fig. 19C, F]. The modification as much represents a change in leverage for the triceps as it does an increase in the subcoracoid muscula-

ture which passed over the expanded shelf separating glenoid and tuberosity. Furthermore there is a change in the shape and orientation of the roughened surface area which gave rise to the triceps tendon. In pelycosaurs it is a convex, narrow strip capping the tuberosity, whereas in cynodonts it is a broad convexity, somewhat triangular in outline and facing posteroventrally. The functional significance of these changes will be discussed in a later section.

The lateral surface of the coracoid is indented to form a shallow fossa for the M. coracobrachialis origin (*cb*, Figs. 18E, 19F, 22A). The fossa extends onto the posteroventral corner of the lateral surface of the procoracoid. In some specimens (Figs. 18E, 22A) the fossa is vertically divided into anterior and posterior halves by a faint convexity. Such a division suggests differentiation of the muscle into a long (posterior) and a short (anterior) head as is common in lizards and *Sphenodon* (Furbringer, 1900).

The ventral margin of the coracoid (Fig. 22D) is a narrow continuation of the rugose surface on the tuberosity for the coracoid triceps. As a rounded edge which continues unchanged across the coracoid-procoracoid suture, its surface lacks laminar bone and its rugose texture is indicative of a cartilaginous extension.

The oval procoracoid is perforated, slightly posterodorsal of center, by a large procoracoid (or supracoracoid) foramen for the transmission of the N. supracoracoideus and blood vessels (*f prc*, Figs. 17, 18, 22). The foramen is sculptured to facilitate passage from a dorsomedial to a ventrolateral direction. The procoracoid plate is thickest at its posterodorsal corner where scapula, coracoid and procoracoid join to form the glenoid. Anterior to this point the width of the sutural contact between scapula and coracoid diminishes. On the lateral surface below the porcoracoid foramen is a hemicircular fossa, open ventrally, representing the origin of the M. biceps (*bi*, Figs. 19F, 22A). A ventrally directed ridge separates this fossa from that of coracobrachialis origin; a more anterior ridge, directed anteroventrally, separates the biceps origin from the remaining lateral surface of the procoracoid from which part of the supracoracoideus arises (*spc*, Figs. 19F, 22A). The ventral margin of the biceps fossa is a sharp, slightly concave keel (Fig. 22D); it connects the rugose and swollen terminal tuberosities of the ridges bordering the fossa, but shows no textural indication of having had a cartilaginous extension. The cranial margin of the procoracoid, between the terminal tuberosity of the anterior ridge and the procoracoid-scapular suture, is reflected laterally to create a very shallow fossa for supracoracoid musculature (Figs. 19F, 22A). The medial surface of the reflected margin (Fig. 22B) is beveled and bears the textured surface typical of cartilaginous overgrowth.

The medial aspect of the coracoid-procoracoid plate (Fig. 22B) is a rather flat surface devoid of prominent features. A shallow fossa below the glenoid buttress of the coracoid is probably associated with the insertion of sterno-costo-coracoid musculature (Fig. 20F). This fossa extends anteriorly for a short distance onto the procoracoid.

Clavicle (Fig. 24)

MATERIAL. Clavicles are adequately known in *Thrinaxodon* (AMMM 5265, SAM K.1395, USNM 22812) and from a collection of disarticulated skeletons of

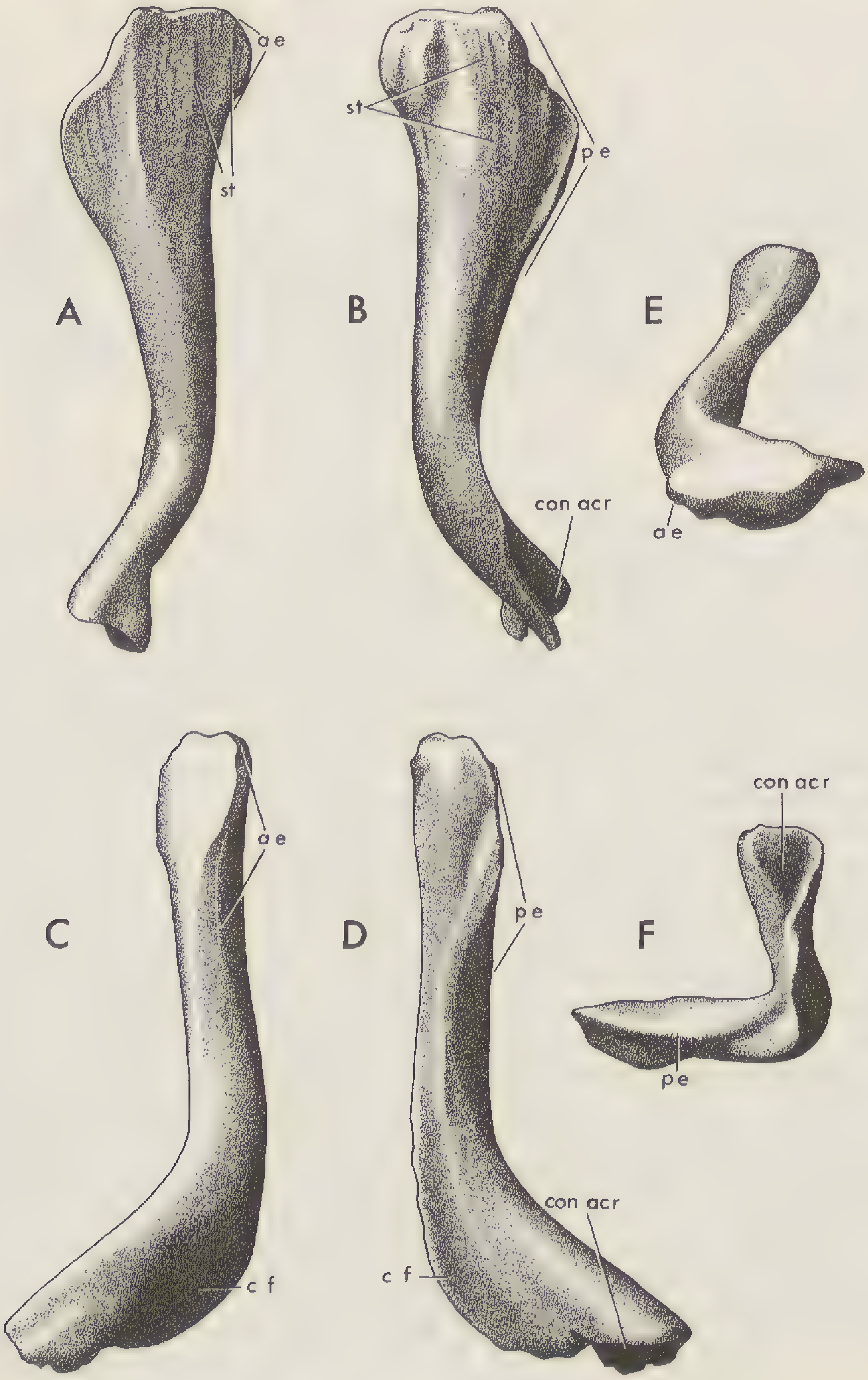

FIG. 24. Right clavicle of cf. ?*Cynognathus* (?*Diademodon*), NMB C.2700. A, dorsal; B, ventral; C, anterior; D, posterior views, with the medial and toward the top of the page. E, medial; F, lateral views. X2/3. Abbreviations: *a e*, anterior edge of medial end of clavicle, possibly the origin of cleido-mastoid musculature; *c f*, clavicular flange; *con acr*, concavity for reception of the acromial process; *p e*, posterior edge of medial half of clavicle; *st*, striations indicating ligamentous or other connective tissue binding clavicle to interclavicle.

Cynognathus and *Diademodon* (NMB C. 2700). Clavicles associated with an interclavicle are known in *Cynognathus* (Broom, 1909) and in a generically indeterminate cynognathid (Watson, 1917a: 24).

MORPHOLOGY. Disregarding minor differences in ossification, cynodont clavicles are morphologically alike and moderately robust. In dorsal view (Fig. 24A) the lateral third of the clavicle is a slender rod directed posterodorsally as well as laterally; the medial two-thirds consists of a gradually expanding, spatulate plate directed medially and horizontally. The long axes of the medial two-thirds and lateral third intersect at an angle of about 145°.

The clavicular facet for the acromion is a concavity formed on the slightly swollen lateral end of the clavicle (*con acr*, Fig. 24B, D, F). The depth of the concavity is accentuated by its thin, protracted edge which is invariably incompletely preserved and may have been continued as a ligament. This edge begins along the posterior aspect of the concavity, runs anterodorsally and then ventrally, thus encircling the top of the concavity but not the bottom. The edge is continued ventrally as a broad flange (*c f*, Fig. 24C, D) that imparts a considerable depth to the lateral third of the bone and probably functioned in the attachment of the clavicular deltoid.

The medial two-thirds of the clavicle is an expanded plate, thickest along its longitudinal axis. Numerous striations (*st*, Fig. 24A, B) parallel to this axis are incised on the dorsal surface and, to a lesser extent, on the ventral surface of the plate. These markings indicate ligamentous or other connective tissue joining the clavicle and interclavicle. The plate is bordered by rather sharply defined edges. The posterior edge of the plate in *Cynognathus* and *Diademodon* gradually arises close to the angle formed between the lateral third and medial two-thirds (*p e*, Fig. 24D) and is longer than the anterior edge (*a e*, Fig. 24C). The anterior edge is differentiated from the cylindrical clavicular shaft more abruptly, arising only near the medial end of the clavicle. To its edge, which is thicker than the posterior edge, may have attached cleidomastoid musculature. In *Thrinaxodon* the posterior edge of the plate is distinct from the clavicular shaft at about the midpoint of the clavicular shaft and therefore is shorter than in larger cynodonts. This gives the medial plate a more symmetrical, spoon-shaped appearance and is the only substantial difference between known cynodont clavicles.

INTERCLAVICLE (Fig. 25)

MATERIAL. The interclavicle is the least well-known element of the cynodont shoulder girdle. Only from *Thrinaxodon* (USNM 22812, Fig. 25A) has the interclavicle been recovered in sufficiently complete condition to permit full description. An isolated anterior fragment of an interclavicle (DMSW R.435), apparently but not certainly from a large cynodont, is available for comparison (Fig. 25B).

Broom (1909: 284) described an interclavicle of *Cynognathus* cf. *crateronotus*, but this specimen was not figured and is apparently lost. Watson (1917a: 25, fig. 9) described and figured an incomplete cynognathid interclavicle associated with a medial

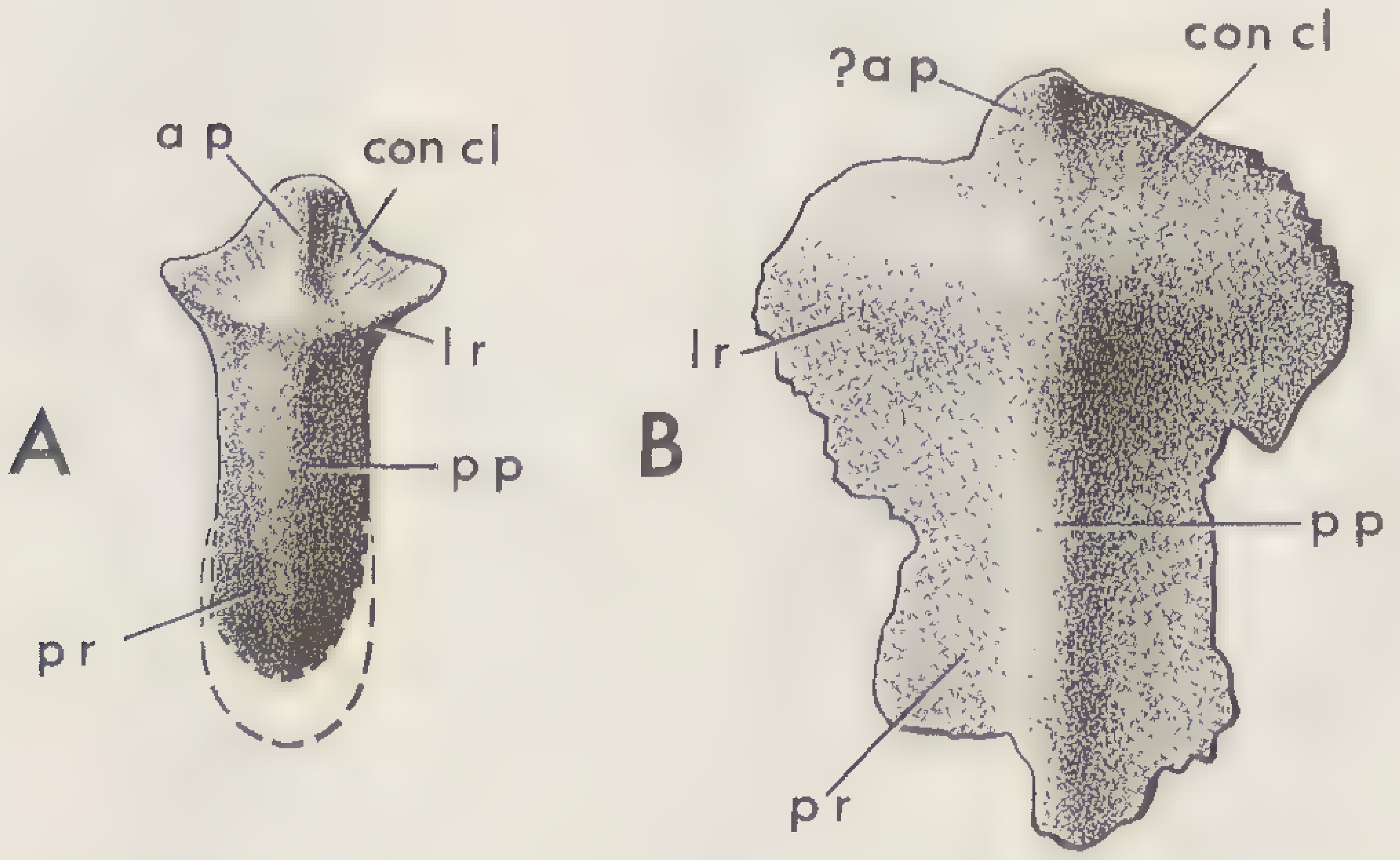

FIG. 25. Incomplete interclavicles of A, *Thrinaxodon* sp., USNM 22812, and B, an unidentified cynodont, DMSW R. 435. Ventral views. X1. Abbreviations: *a p*, anterior ridge, possibly for origin of part of pectoralis musculature; *con cl*, concavity for articulation with medial end of clavicle; *l r*, lateral ridge, delineating posterior border of concavity which receives the medial end of the clavicle; *p p*, posterior ridge, probable site of origin for the part of pectoralis musculature; *p r*, posterior ramus.

end of a clavicle. The specimen is possibly DMSW R.435, described below. The interclavicle of *Leavachia duvenhagei* (RC 92), originally described by Broom (1948: 623, fig. 40), is morphologically very similar to that in *Thrinaxodon*, although proportionately somewhat wider.

MORPHOLOGY. The interclavicle of *Thrinaxodon* is cruciate with a long posterior ramus. In ventral view (Fig. 25A) the anterior half bears a median tuberosity from which radiate four ridges; on either side two ridges pass anterolaterally (*l r*), while the remaining two pass directly anteriorly (*a p*) and posteriorly (*p p*), respectively. The anterior and lateral ridges define bilateral, triangular concavities for reception of the medial ends of the clavicles (*con cl*, Fig. 25A). The floor of these concavities is striated, just as are the medial clavicular extremities, indicating the presence of cartilage or perhaps ligamentous connective tissue. The anterior ridge (*a p*) separating the two concavities is a thin lamina of bone with vertical sides. The posterior ridge (*p p*), probably the site of origin for pectoral musculature, is most prominent anteriorly and gradually attenuates posteriorly. The posterior margin of this specimen is missing and was apparently very thin, but gives the impression that it widened transversely to a spoon-shaped terminus. Broom (1909: 284) noted a distinct widening of the posterior part of the interclavicle in *Cynognathus*, as did Watson (1917a: 25) for another cynodont interclavicle.

On the interclavicular fragment of the unidentified cynodont (Fig. 25B) most of the above named features, insofar as they are not obscured by breakage, are repeated. Yet none of the original edges of this specimen are preserved so the extent of the ridges cannot be compared to those in *Thrinaxodon*. The anterior ridge appears to be proportionally not as prominent as in *Thrinaxodon*, but this may be an artifact of

breakage. A tubercle at the anterior extremity of the bone may represent the posterior extremity of a typical galesaurid type of ridge (?*a p*, Fig. 25B).

The cruciate pattern of the cynodont interclavicle is a certain mark of pelycosaurian heritage. Except for the slightly greater width of the posterior ramus, the interclavicle of *Thrinaxodon* essentially duplicates the interclavicular morphology of *Dimetrodon* (see Romer and Price, 1940: 118). However not all cynodont interclavicles retain a primitive pattern. The interclavicle of the *Exaeretodon*, a South American transversodontid, is short and triangular in form and bears a deep, median keel (Bonaparte, 1963a). Its morphology is clearly a specialized feature peculiar to this cynodont genus. The position of the keel is suggestive of a homology with the anterior ridge of the interclavicle described above. If so, the traversodontid keel might represent ossification of a plate which in galesaurids and other cynodonts was a cartilaginous (ventral) extension of the anterior ridge. Such a ridge, whether osseous or cartilaginous, would serve as an extensive area of origin for a massive pectoralis complex. Certainly the deltopectoral crest of the *Exaeretodon* humerus is no more robust or extensive than in other cynodonts, which is indirect evidence that the muscular attachments were not substantially different in traversodontids. The absence of a large interclavicular keel in non-traversodontid cynodonts might be explained on the basis of its having been cartilaginous. Otherwise it is difficult to account for the sudden appearance of this feature in traversodontids whose postcranial skeleton, for the most part, is little modified from a typical cynodont pattern.

2. FORELIMB

Humerus (Figs. 26–28)

MATERIAL. Humeri are adequately known in *Thrinaxodon* (SAM K.1395, AMMM 5265, USNM 22812, BPI 376 and NMB specimens described by Brink, 1954), in *Galesaurus* (SAM K.1119) and in *Diademodon* and *Cynognathus* from two collections where disarticulated skeletons of these two genera are preserved together (BPI 1675, NMB C.2693). Except for differences in size and ossification, all humeri are morphologically similar. In the National Museum (Bloemfontein) collection of *Diademodon* and *Cynognathus* (NMB C.2693), 17 complete or nearly complete humeri range in size from 58 to 178 mm. No consistent morphological differences among these bones could be discerned by which two genera might be distinguished, yet abundant cranial fragments attest to the presence of both genera. The conclusion is inescapable that the humeri of *Diademodon* and *Cynognathus* are essentially identical, although it is possible that large samples might show consistent differences in size.

The humeri of *Cricodon metabolus* and *Scalenodon augustifrons* were described by Crompton (1955b: 626, 652) and are morphologically indistinguishable from other large cynodont humeri. Incomplete humeri, also from the Manda Formation, are described by von Huene (1950), but these dissociated specimens are generically indeterminate.

Other known cynodont humeri are either referable to one of the above genera or are too poorly preserved or prepared to make adequate comparisons. Owen (1876: 21, Pl. XIX) described and figured the humerus of *Cynochampsa laniarius* (BMNH S.A. 43), the genus questionably synonymized with *Diademodon* by Watson and Romer (1956: 65). The humerus could be either that of a gomphodont or a cynognathid.

Seeley (1895a: 27–31) described a large humerus associated with *Gomphognathus* sp. (=*Diademodon*, see Brink, 1955, and Watson and Romer, 1956: 65), but admitted that it is so similar to that of *Cynognathus* that it might belong to this genus.

Seeley (1895a: 44–45) also described the well-preserved humerus of *Microgomphodon eumerus* (BMNH R.3581), but Brink (1955: 31) correctly recognized that this specimen probably represents a juvenile *Diademodon*.

Parrington's (1934) description of the humerus of *Galesaurus* (UMC R.2722) in fact was based on material which cannot be positively assigned to this genus (see above, p. 62). The material is unquestionably galesaurid, however, and does not differ from the *Thrinaxodon* pattern except for a slightly larger size. The same statement can be made of all other limb and girdle elements associated with this specimen.

The humeri from a disarticulated skeleton of *Glochinodontoides gracilis* (TM 83), described by Haughton (1924), are poorly preserved and only incompletely prepared. No substantial morphological differences are evident with which to contrast these humeri with those of the larger cynognathids and gomphodonts or those of the smaller galesaurids. The apparent reduced thickness of the proximal end, when compared to that in *Cynognathus* or *Diademodon*, is due to the lack of ossification of the head which is typical of smaller cynodonts.

Broom (1948: 623–624, fig. 42) described and figured the humerus of the procynosuchid *Leavachia duvenhagei* (RC 92). From his description it would appear to differ from other cynodont humeri only in having a longer and more prominent ectepicondylar flange. However, Brink and Kitching (1953a: 313–314), who performed additional preparation on this specimen, mentioned several inaccuracies in Broom's description of other skeletal elements and therefore Broom's figures are suspect. Now that the material is better prepared, it is obvious that the distal end of the humerus is entirely comparable to that in other cynodonts. Furthermore Broom claimed that the humeral length is 80 mm and the distal end width is 29 mm, giving a smaller length-width ratio (.36) than is typical of cynodonts (about .50). Measurements taken from his illustration (fig. 52, natural size), however, give a length of 79.5 mm and a distal width of 44 mm, yielding a ratio of .55 which is more comparable to that of other cynodonts.

MORPHOLOGY. Cynodont humeri more closely resemble those of primitive tetrapods in general and pelycosaurs in particular than those of any therian. In broad aspect the cynodont and monotreme, especially echidna, humerus are similar, but proportionally the monotreme humerus is much wider. This and other differences in morphological detail are probably the result of the latter's fossorial specialization and make a detailed comparison between the two of dubious value as far as interpreting cynodonts is concerned.

Humeral lengths range from about 3 cm in *Thrinaxodon* to about 20 cm in *Cynognathus* sp. The maximum width between epicondyles is invariably about one-half the

length of the bone; femora of South American cynodonts were apparently more variable with regard to this feature (*Exaeretodon*, 54%; *Chiniquodon*, 58%; *Massetognathus*, 40%. See Bonaparte, 1963a, Romer, 1969a, Jenkins, 1970a). Maximal proximal width measured from the lesser tuberosity to deltopectoral crest is consistently 40% of total length. In cynodonts the inferred insertions of the Mm. supracoracoideus and subcoracoscapularis are not marked by actual (greater and lesser) tuberosities as are their homologues in mammals, Mm. spinati and subscapularis, respectively. However it is convenient to use this nomenclature in reference to these loci of insertion. The cynodont "lesser tuberosity" is best illustrated in Figure 26D as a bulbous area (*l t*) on the proximal, actually proximomedial, aspect of the humerus.

The broad deltopectoral crest constitutes about half the width of the proximal end (*d c*, Figs. 26–28), and the flaring of the epicondyles account for the distal breadth (*ec*, *en*, Figs. 26–28). The distal half of the humerus, triangular in outline, is essentially planar. The proximal half of the humerus is composed of two planes, the deltopectoral crest and the adjacent shaft, which intersect along the board bicipital groove at an angle of approximately 135° (*bi gr*, Fig. 27A). The short shaft connecting the expanded proximal and distal ends is triangular in cross-section and is only about ten percent of the total humeral length. The long axes of the two ends are "twisted" about the humeral axis so that in proximal view (Figs. 27A, 28D) they intersect at a 40 to 50° angle. The symmetry of the humerus is further complicated by dorsal flexure of the proximal half of the shaft (Figs. 26C,D, 28E,F).

The humeral head in all known specimens of *Thrinaxodon* and *Galesaurus* is incomplete and rather flat due to the fact that its terminus was extensively cartilaginous (*h*, Fig. 28A,D). There is no reason to believe, however, that the structure was different from that of larger cynodonts in which the head is better ossified. As preserved in *Diademodon* and *Cynognathus*, the humeral head is a low convexity centered on the strap-shaped surface of the proximal end (*h*, Fig. 27A). On average the articular surface faces anteromedially and somewhat dorsally. A dorsolaterally reflected lip raises the articular facet above the dorsal surface of the shaft (*l h*, Fig. 26A,C). Ventrally the articular facet is terminated along a clearly defined edge by intersection with the bicipital groove (Fig. 26B). The anterior (or lateral) and posterior (or medial) limits of the head are not obvious in most specimens because the surfaces of the head and adjacent tuberosities are confluent along the narrow, strap-shaped surface of the proximal end. The roughened texture of this entire surface indicates a cartilaginous overgrowth. The insertion of the M. subcoracoscapularis (lesser tuberosity) is inferred to be medially adjacent to the head on the bulbous proximomedial corner of the humerus (*l t*, Fig. 26A,B,D). In several specimens (NMB C.2693) the lesser tuberosity appears to be set apart from the head by a slight depression cutting across the strap-shaped end surface on which both are situated (Fig. 27A). The insertion of the M. supracoracoideus (greater tuberosity) is inferred to be on the proximolateral corner of the humerus at the junction of the head and deltopectoral crest (*g t*, Fig. 26A-C). This corner, unlike the proximomedial corner, is broadly rounded and narrow. The rugose surface continues distally along the deltopectoral crest for almost one-third of its length.

The deltopectoral "crest" is a rather rectangular flange, thickest along its junction with the shaft (*d c*, Figs. 26-28). The relatively thick proximal third of its free margin

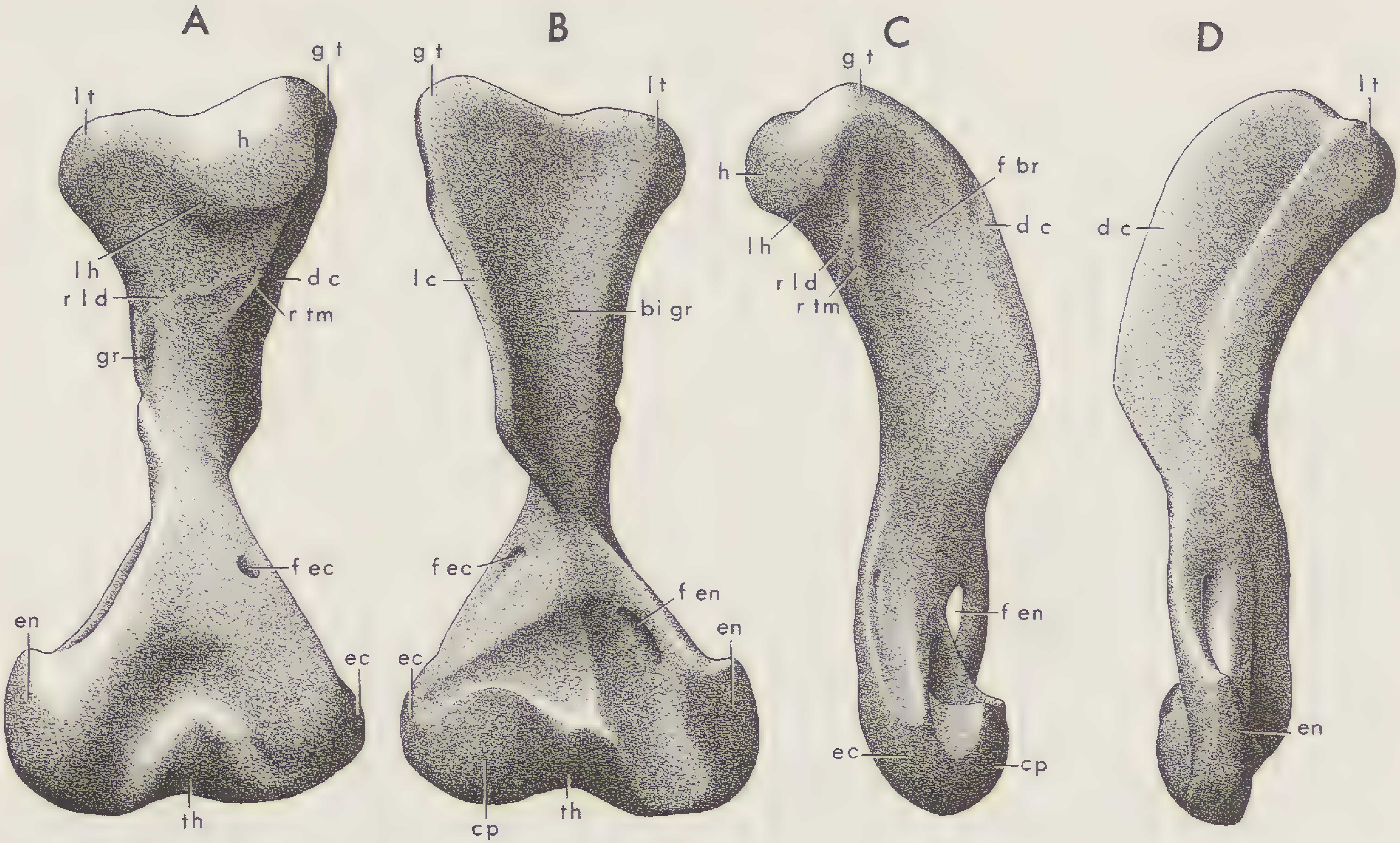

FIG. 26. Part I. Right humerus of cf. ?*Cynognathus* (?*Diademodon*), NMB C.2693, in A, dorsal; B, ventral; C, anterolateral; D, posteromedial views. X1.

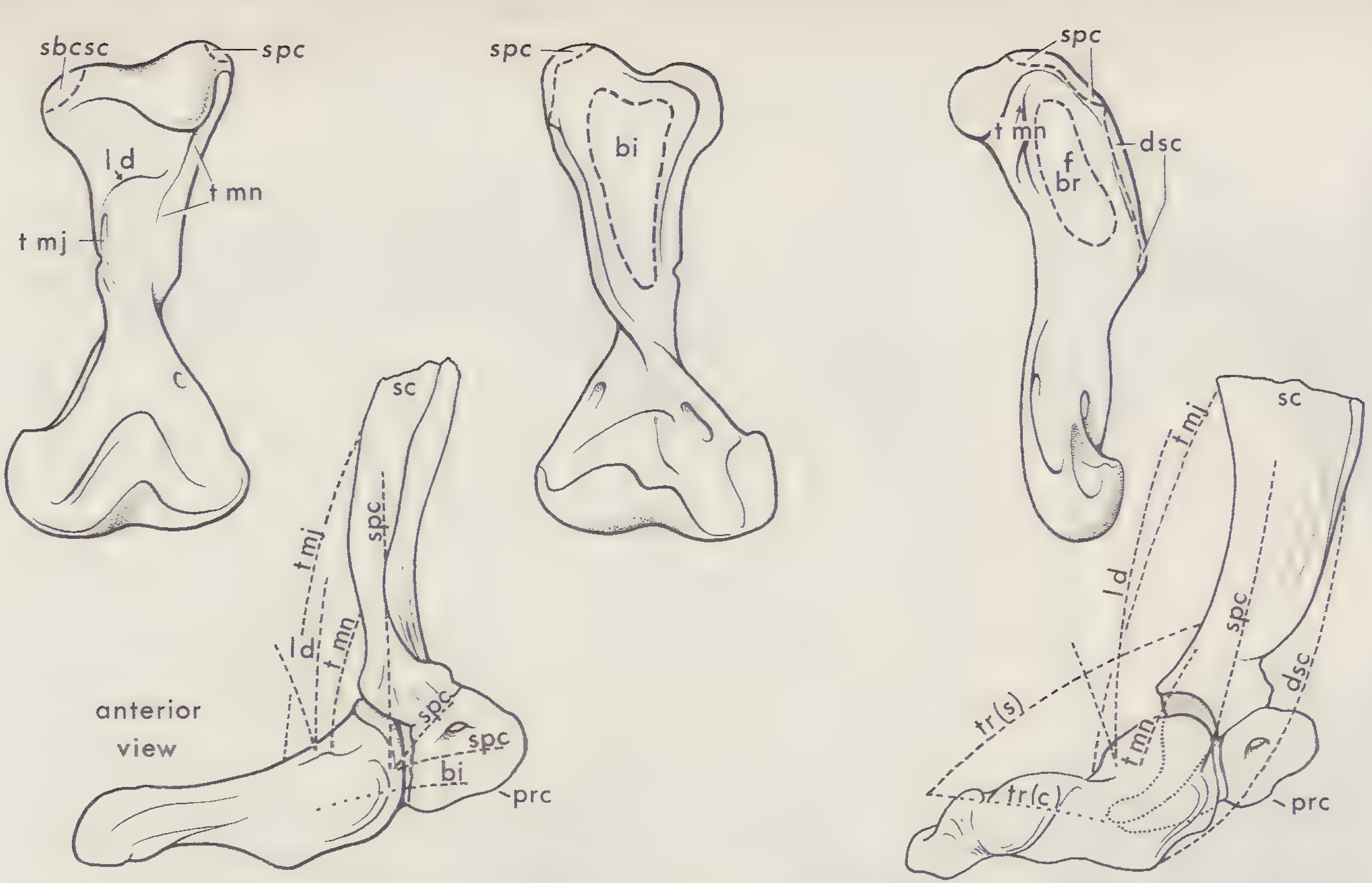

FIG. 26. Part II. The line drawing above gives reconstructed muscle insertions and, below, the presumed orientation of some of the shoulder muscles in anterior and lateral views. Abbreviations: *bi*, biceps; *bi gr*, bicipital groove; *cp*, capitulum; *d c*, deltopectoral crest; *dsc*, dorsoscapularis; *ec*, ectepicondyle; *en*, entepicondyle; *f br*, fossa probably related to brachialis origin; *f ec*, ectepicondylar foramen; *f en*, entepicondylar foramen; *g t*, greater tuberosity; *gr*, groove possibly representing the insertion of the teres major; *h*, humeral head; *l d*, latissimus dorsi; *l h*, dorsal lip of the humeral head; *l t*, lesser tuberosity; *p*, pectoralis musculature; *prc*, procoracoid; *r l d*, ridge possibly representing the insertion of the latissimus dorsi; *r tm*, ridge possibly representing the insertion of the teres minor; *sbcsc*, subcoracoscapularis; *sc*, scapula; *spc*, supracoracoideus; *th*, trochlea; *tr (c)*, coracoid head of triceps; *tr (s)*, scapular head of triceps; *t mj*; teres major; *t mn*, teres minor.

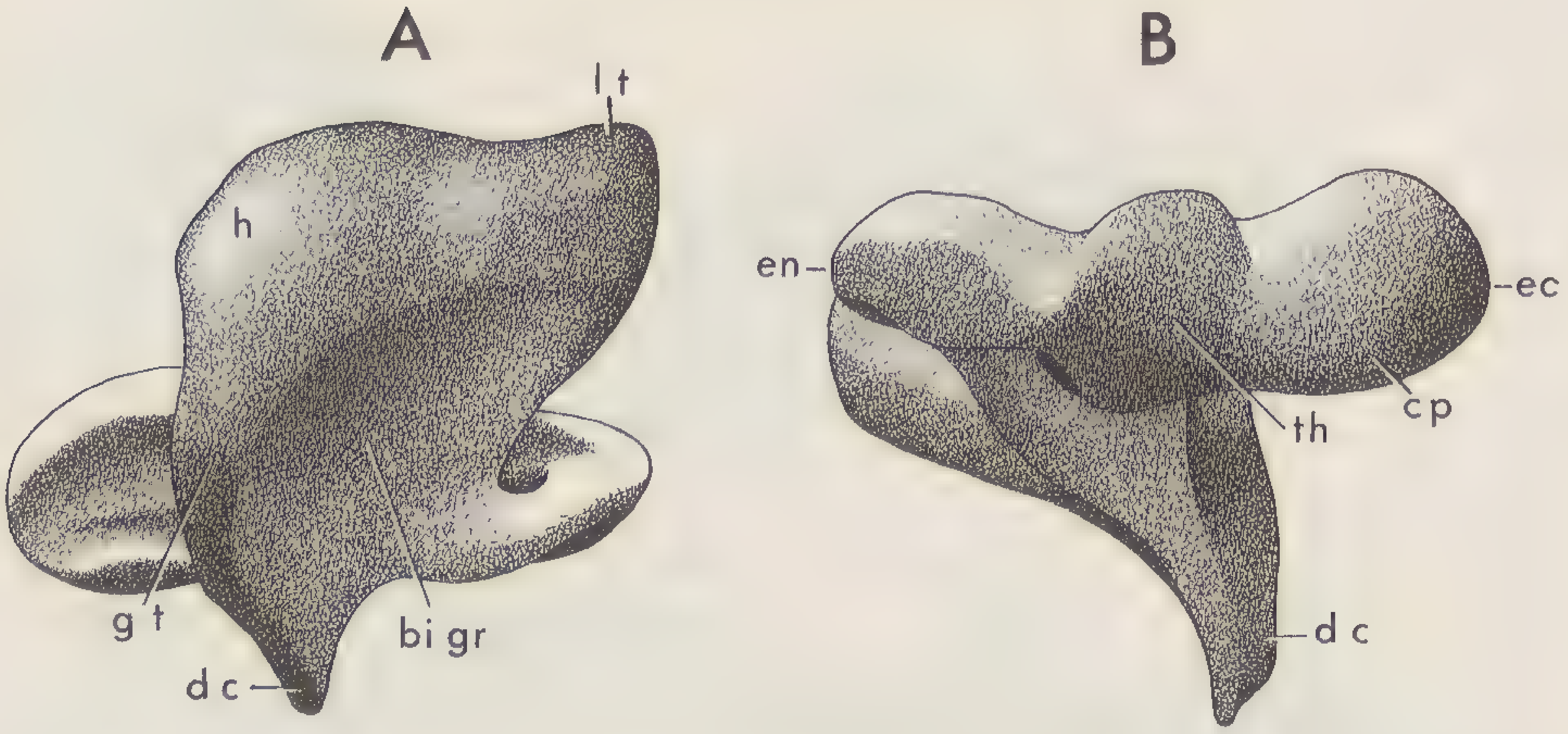

FIG. 27. A, proximal; B, distal views of humerus illustrated in FIG. 26. X1. Abbreviations as in FIG. 26.

was probably occupied by supracoracoid insertion. The remainder of the margin is beveled on both sides, creating a sharp edge bowed slightly ventrally (Fig. 26B,C). The flange abruptly terminates at a small marginal tuberosity equidistant from the proximal and distal ends of the humerus; from this tuberosity a low ridge runs posterodistally to bridge the entepicondylar foramen.

Deltoid musculature may be reconstructed as inserting on the beveled anterolateral margin and terminal tuberosity of the deltopectoral crest. The entire posteromedial margin of the crest margin bears a pattern of striations and rugosity which may indicate the M. pectoralis insertion. The entire anterolateral surface of the deltopectoral crest is occupied by a shallow but broad fossa (*f br,* Figs. 26C, 28E) probably representing the origin of the M. brachialis. A prominent ridge runs anteroproximally between the fossa and the humeral head (*r tm,* Fig. 26A) and may possibly indicate the insertion for a teres minor.

From the ridge just described another ridge runs obliquely across the dorsal surface of the humeral shaft (*r l d,* Fig. 26A). It is low and irregular and conceivably represents the insertion for the M. latissimus dorsi. A groove, more distally placed, parallels the shaft along its posteromedial aspect (*gr,* Fig. 26A). In one excellently preserved specimen (BPI 1675) it is clear that the irregular ridge and groove are confluent, and therefore the groove may represent the initial differentiation of the insertion of the M. teres major from that of the M. latissimus dorsi. It is equally possible that one or both of these features represents the origin of one of the humeral triceps heads.

Oval entepi- and ectepicondylar foramina pass distoventrally through the bone adjacent to the epicondyles and each is obliquely inclined away from the shaft. Broom (1948: 624) claimed than an ectepicondylar foramen is absent in *Thrinaxodon,* but it is clearly present in all known specimens except where lost through breakage. The ectepicondylar foramen (*f ec,* Figs. 26A, 28A) is at least half the size of the other and is enclosed by a thin flange with a slightly swollen margin. Romer (1922b: 538–539) suggested that the ectepicondylar foramen was formed during the course of distal

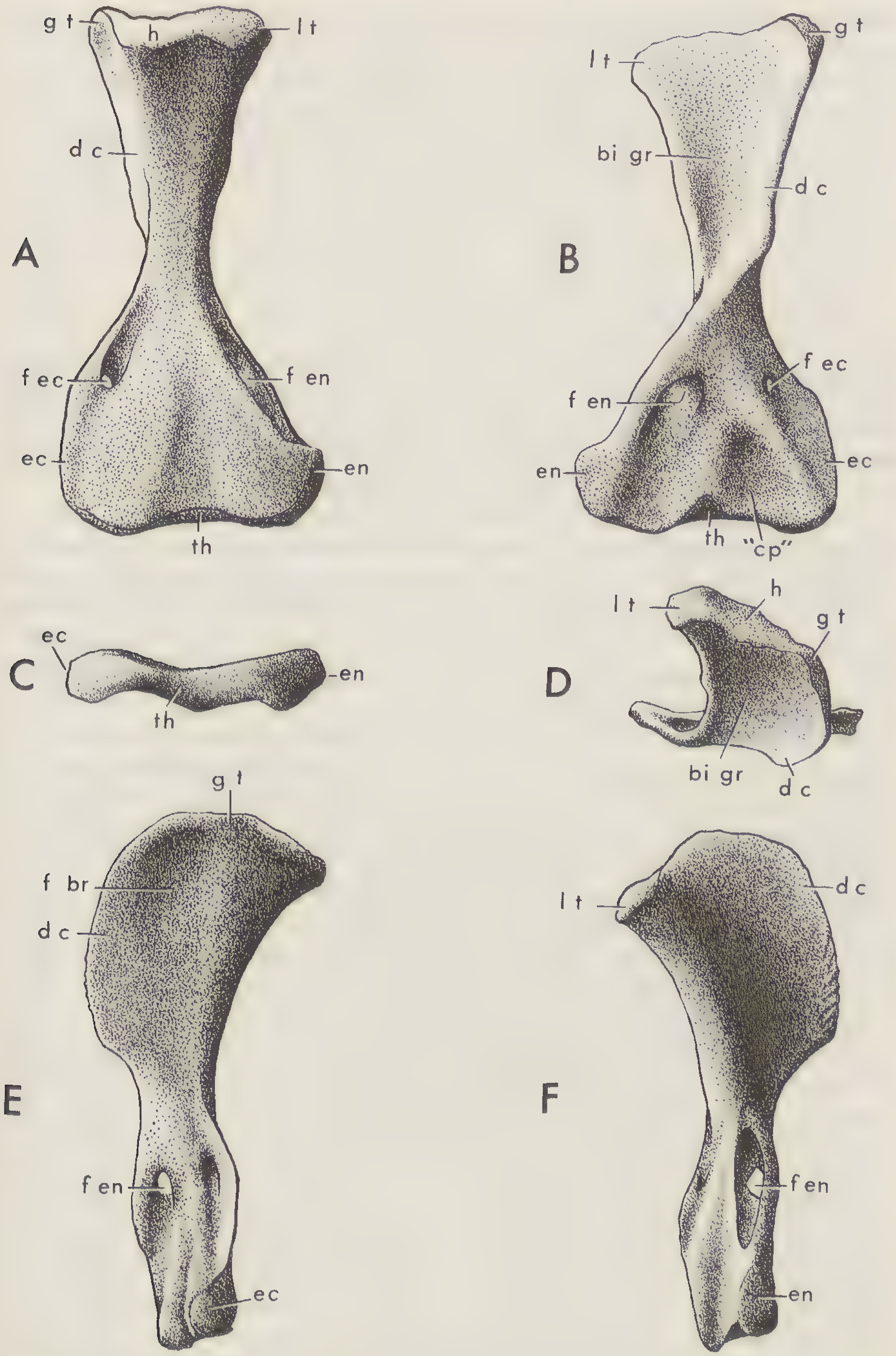

FIG. 28. Left humerus of *Thrinaxodon*, SAM K. 1395, in A, dorsal; B, ventral; C, distal; D, proximal; E, anterolateral; F, posteromedial views. X2. Abbreviations as in FIG. 26 except: *"cp"*, area of humeroradial articulation, with capitulum not preserved as a rounded eminence.

migration of supinator musculature. In most pelycosaurs the supinator tuberosity on the shaft and the ectepicondyle are separated by a groove through which passed a branch of the radial nerve. With further elongation of the shaft in later forms the musculature arising from the supinator tuberosity migrates distally with the extensor muscles and the radial nerve is enclosed by a bony flange which permits muscular origin in the region around the nerve. In most mammals the foramen is completely lost, but in *Didelphis* there often occurs a proximal groove in the supinator crest which represents the distal half of the "bypassed" foramen. In cynodonts the foramen is proximally placed and therefore closely approximates a mammalian condition.

The long, oval entepicondylar foramen is enclosed by a stout rod of bone which, as noted before, is the distal continuation of the deltopectoral flange. Romer (1922b: 557) suggested that its formation in primitive tetrapods resulted from the proximal expansion of flexor musculature. The median nerve became enclosed by the proximal extension of bone surface required for flexor origins. This foramen is lost in most mammals, but is retained in the more primitive forms such as *Didelphis* where its form and orientation are almost identical with that in cynodonts.

The entepicondyle is a stout process bearing a curved, strap-shaped terminal margin (*en*, Fig. 26D). The margin is rugose in texture, indicating cartilaginous extension, and extends from near the distal extremity of the entepicondylar foramen around to the trochlea (Fig. 27B). The entepicondyle is displaced farther from the radio-ulnar facet than is the ectepicondyle and as a result the triangular distal end of the humerus is somewhat asymmetrical. This condition parallels that in monotremes and increases the flexor leverage in the forearm.

In the larger cynodonts the ectepicondyle is a broad swelling on the distolateral corner of the humerus (*ec*, Fig. 26C). Its thickness, which is greater than that of the entepicondyle (*en*, Fig. 27B), possibly correlates with its position partially overlying the capitulum and the need for a strong buttress for weight transference to the radius. In smaller cynodonts such as *Thrinaxodon* in which weight was not such a critical factor, the ectepicondylar thickness is less than that of the entepicondyle (Fig. 28C). In no cynodont does the rugose terminal surface for forearm extensor musculature origin extend as far proximally as does the similar surface of the entepicondyle. However extensor origins may have continued proximally along the thin ectepicondylar flange (or ridge) which bridges the ectepicondylar foramen.

The trochlea in *Diademodon* and *Cynognathus* is a broad groove occupying about one-quarter of the total distal end width (*th*, Fig. 27B). It is extended onto the dorsal and ventral aspects of the humerus by lips raised above the respective surfaces (Fig. 26A,B); the ventral lip, somewhat wider than the dorsal, merges with the adjacent capitulum. From dorsal to ventral extremities the trochlea turns an angle of 180°. Its dorsoventral axis (seen in end view) is oblique to the long axis of the distal end, i.e., the dorsal lip is more anteriorly situated than the ventral (Fig. 27B). In *Thrinaxodon* and *Galesaurus* the trochlea is not well ossified (*th*, Fig. 26A-C), but in view of the other close similarities between cynodont humeri, it seems probable that the trochlea in these genera was essentially identical to that of larger forms.

The capitulum in *Diademodon* and *Cynognathus* is a board, low convexity occupying almost forty percent of the total distal end width (*cp*, Fig. 26B). The facet is entirely confined to the ventral aspect of the humerus where its rugose surface is con-

fluent posteromedially with the trochlea and anterolaterally with the ectepicondyle. In *Thrinaxodon* and *Galesaurus* the capitulum is a round concavity in the same position ("*cp*", Fig. 28B). It appears probable that this is due to a lack of ossification of a bulbous facet which, as in larger forms, articulated with the slightly concave proximal facet of the radius.

Radius (Figs. 29, 30)

MATERIAL. Cynodont radii are known in *Thrinaxodon* (SAM K.1395), *Galesaurus* (SAM K.1119), and *Cynognathus* and *Diademodon* from two collections (BPI 1675, NMB C.2697) in which disarticulated skeletons of these two genera are preserved together. Broom (1948: 625) gave a diagrammatic figure and an inadequate description of the radius in *Leavachia duvenhagei* (RC 92); comparison of the procynosuchid radius with that of later cynodonts must await further study.

MORPHOLOGY. The cynodont radius (Figs. 29, 30) is a simple, cylindrical bone with expanded ends and in general aspect resembles a pelycosaur radius. The distal half of the shaft is curved slightly medially to facilitate passage of the radius over the anterodistal surface of the ulna. In larger cynodonts the proximal articular facet is hemicircular, with a straight edge along the posteromedial aspect. The facet surface is concave anteroposteriorly and slopes medially (*pr ar f*, Fig. 29C). In *Thrinaxodon* and *Galesaurus* the poorly ossified proximal end is an even, very shallow depression, but in outline and in orientation it resembles that of larger cynodonts (*pr ar f*, Fig. 30A,C).

In larger cynodonts a tuberosity occurs on the posteromedial aspect of the proximal end below the capitular facet (Fig. 29B). This tuberosity bears a facet (*f u*, Fig. 29A,B) for articulation with the radial notch of the ulna. In mammals the same facet forms a strap-shaped circumference around the radial head for 180° or more. The circumferential extent in cynodonts appears to have been on the order of 70°-90°, and the degree of pronation and supination possible must have been correspondingly less than in most mammals. The same tuberosity and facet in *Thrinaxodon* (*f u*, Fig. 30B) and *Galesaurus* is inconspicuous and would be overlooked if the better ossified radii of larger cynodonts were not available.

A ridge (*r*, Figs. 29B,C, 30B,C) from the anterior aspect of the ulnar facet passes down the posteromedial side of the shaft. It gradually attenuates and is lost near the middle of the shaft. In larger cynodonts the ridge bears a distinct swelling at about its midpoint which may represent a radial tuberosity for insertion of the biceps. Medial to this swelling is a fossa (*r f*, Fig. 29B,C) possibly also representing the insertion of a major antebrachial flexor. Two faint lineations, each representing a muscular or ligamentous "scar", run obliquely down the shaft from the swelling. The posterior (*pl*, Fig. 29B,D) is the longer of the two, traceable in larger cynodonts to nearly the distal end. Its position suggests that it is the origin of a flexor muscle. In *Galesaurus* (SAM K.1119) and in *Thrinaxodon* this feature is represented by a distinct crest (*pl*, Fig. 30D). The anterior lineation (*al*, Fig. 29C) rather closely parallels the anterior crest

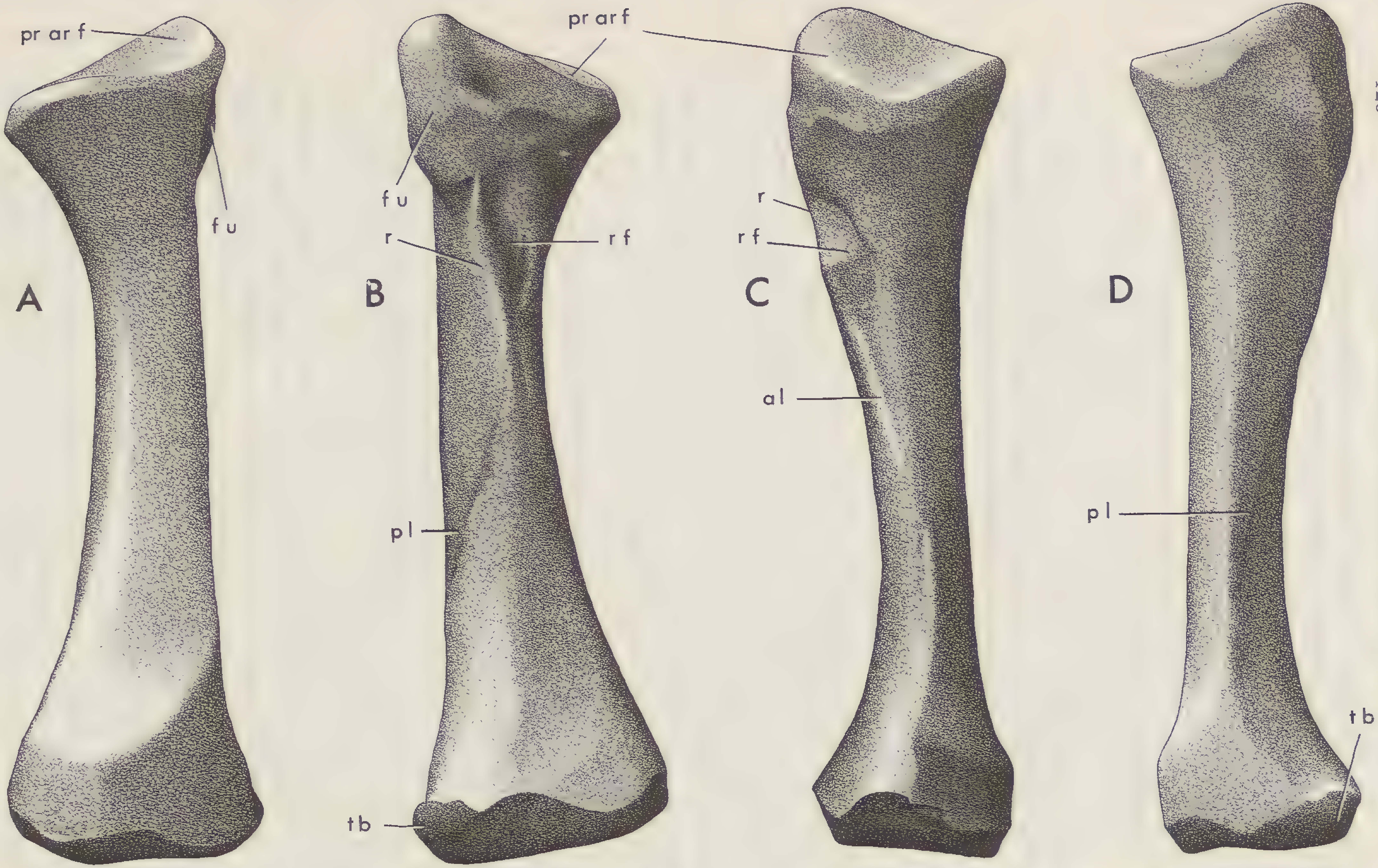

FIG. 29. Left radius of cf. ?*Cynognathus* (?*Diademodon*) BPI 1675 in A, anterior; B, posterior; C, medial; D, lateral views. X1. Abbreviations: *a l*, anterior lineation; *f u*, facet for articulation with radial notch of ulna; *p l*, posterior lineation; *pr ar f*, proximal articular facet; *r*, ridge bearing radial tuberosity; *r f*, fossa possibly representing the insertion of an antebrachial flexor; *tb*, tuberosity for ulnar contact.

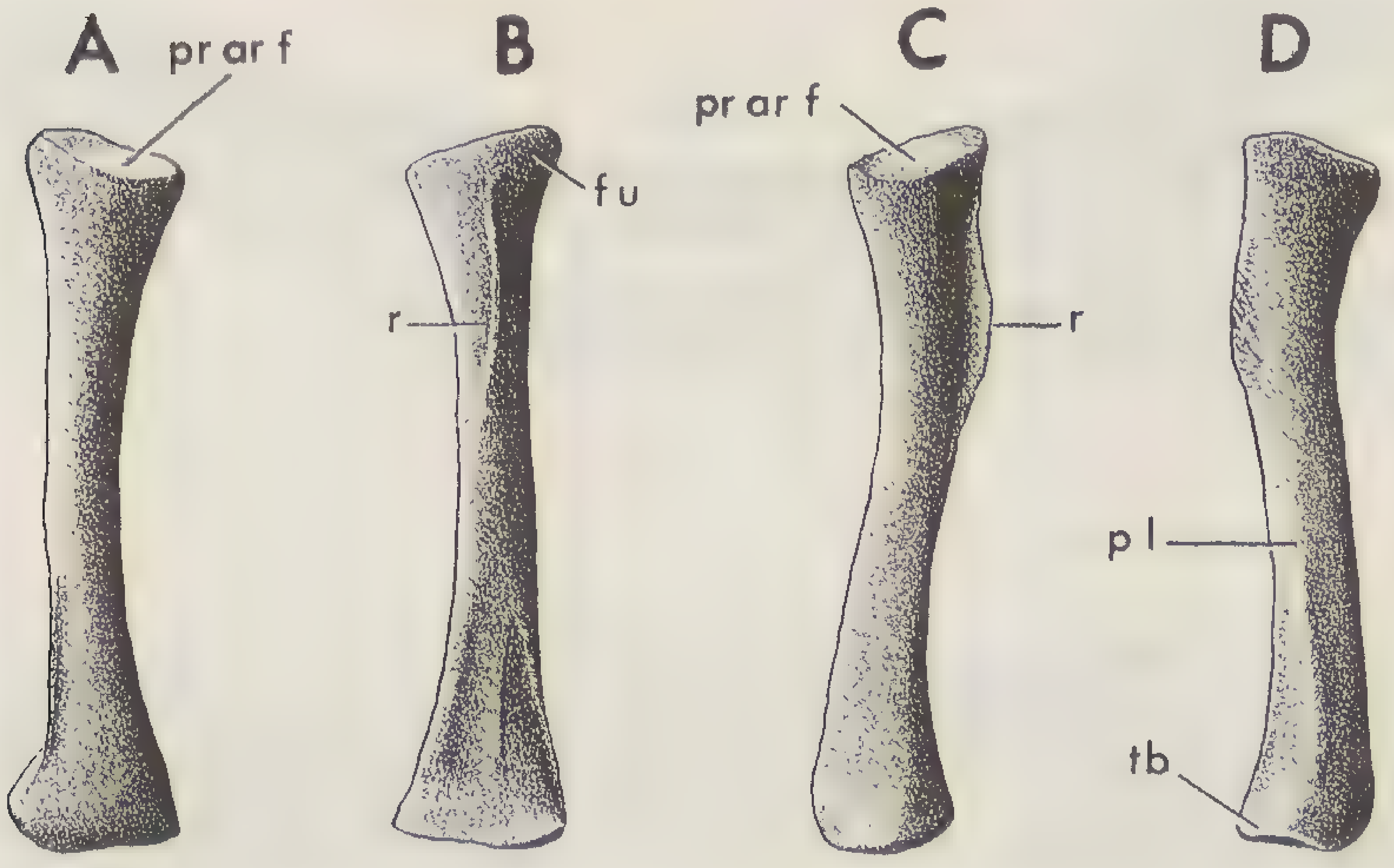

FIG. 30. Right radius of *Thrinaxodon*, SAM K. 1395, in A, anterior; B, posterior; C, medial; D, lateral views. X2. Abbreviations as in FIG. 29.

of the ulna from which a radio-ulnar interosseous ligament probably arose. This lineation perhaps represents the radial attachment of this ligament.

The distal end of the radius is triangular in outline. The articular facet is a shallow depression approximately equal in area to that of the proximal end. The rim of the facet was apparently cartilaginous and therefore is not preserved in any specimen. Along the posterolateral aspect of the rim is a tuberosity (*tb*, Fig. 29B,D) which apparently made contact with the anteromedial aspect of the distal end of the ulna.

ULNA (Figs. 31, 32)

MATERIAL. Cynodont ulnae are known in *Thrinaxodon* (AMMM 5265, SAM K. 1395, BPI 287, BPI 376), in *Galesaurus* (SAM K.1119), and in *Cynognathus* and *Diademodon* from two collections in which the disarticulated skeletons of these two genera are preserved together (BPI 1675, NMB C.2695). Broom's (1948: 624–625) description of the ulna in *Leavachia duvenhagei* (RC 92) was criticized by Brink and Kitching (1953a: 314) for inaccuracy but no specific corrections or redescription were given. Brink and Kitching's figure shows the ulna, although incompletely exposed, is apparently similar in morphology and proportion to those of other cynodonts.

MORPHOLOGY. The cynodont ulna is short and robust relative to typical mammalian ulnae. The only major difference between the ulnae of galesaurids and larger cynodonts is that the former are consistently more slender and gracile (cf. Figs. 31 and 32). In addition to this basic proportional difference galesaurid ulnae are not as well ossified as in larger cynodonts; a detailed comparison of features would reveal many apparent differences, but in fact most of these are the result of differences in degree of ossification.

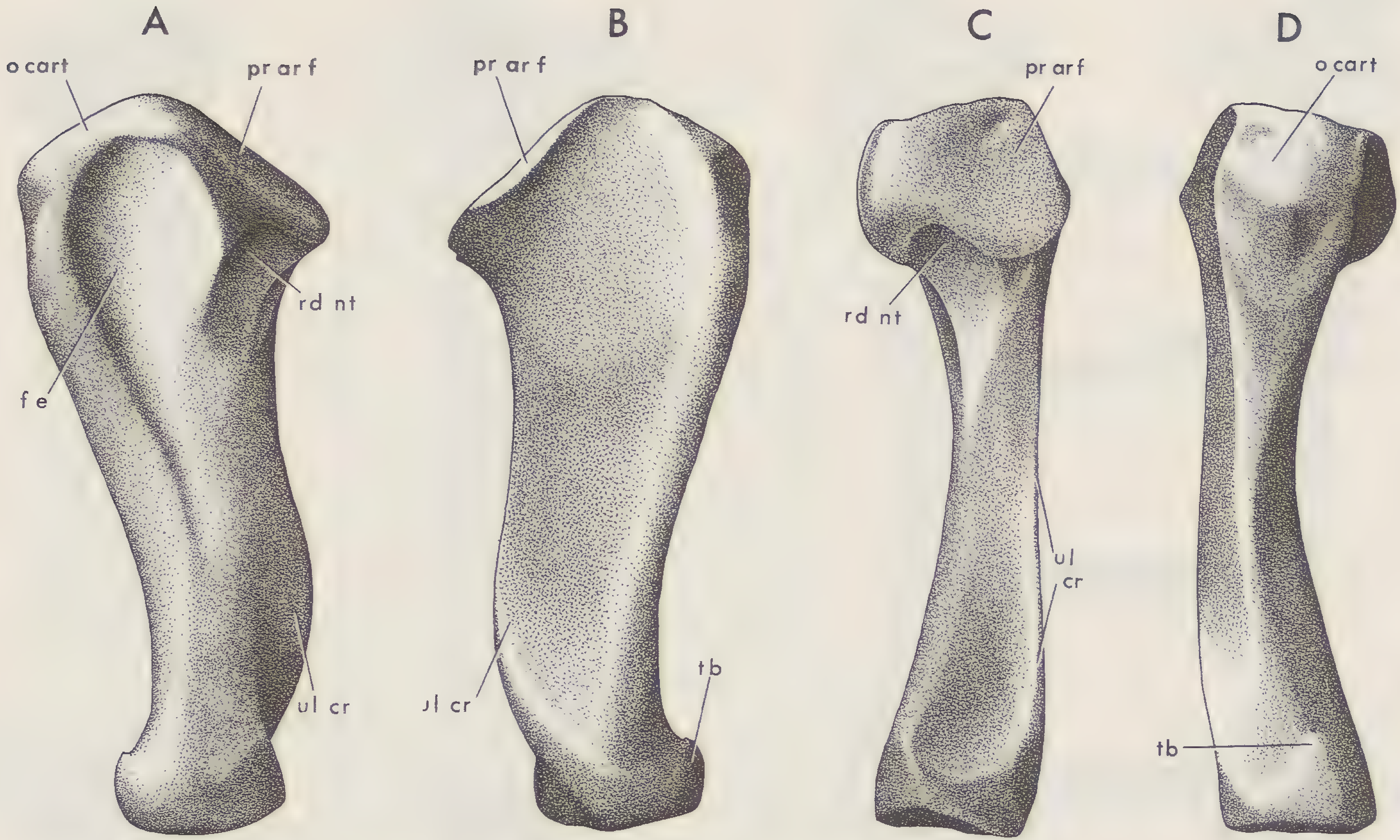

FIG. 31. Right ulna of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, in A, lateral; B, medial; C, anterior; D, posterior views. X3/4. *f e*, fossa presumably for an extensor muscle origin; *o cart*, osseous base from which a presumably cartilaginous olecranon process arose; *pr ar f*, proximal articular facet; *rd nt*, radial notch; *tb*, tubercle possibly representing the attachment of an extensor muscle; *ul cr*, ulnar crest.

In lateral view the sigmoidal shape resembles the outline of generalized mammalian ulnae, but a high crest (*ul cr*, Figs. 31A–C, 32A–C) along the anteromedial margin imparts a depth to the bone quite uncharacteristic of mammalian proportions. In anterior view (Figs. 31C, 32C) the shaft is very narrow, with the distal end evenly expanding mediolaterally and the proximal end expanding primarily laterally.

An ossified olecranon is absent. The proximal end of the ulna, homologous with the point where an olecranon develops in mammals, is very wide and the bone is cancellous (*o cart*, Figs. 31A,D, 32B,D). A broad, cartilaginous olecranon appears a probability on this evidence (see Fig. 42) but is virtually necessitated by previously cited evidence for well-developed triceps musculature, especially the coracoid head.

The cartilaginous olecranon probably contributed to the formation of a hemicircular semilunar notch. As preserved, however, the "notch" is merely a very slightly concave, oval facet (*pr ar f*, Fig. 31A–C) adjoining the surface from which the inferred olecranon arose. The facet as a whole is inclined anteriorly (relative to the shaft axis) at an angle of 45° but also slopes laterally to a small degree.

On the lateral surface of the proximal end are two fossae which are invariably well developed. The anterior and smaller of the two (*rd nt*, Fig. 31A), analogous to the "radial notch" of mammals, is limited to a triangular area immediately distolateral to the sigmoid facet and receives the tubercle on the proximal end of the radius. This fossa is poorly developed in galesaurids. The posterior fossa (*f e*, Figs. 31A, 32A) is a smooth, spoon-shaped depression which abruptly attenuates distally and terminates between the middle and distal thirds. In galesaurids it commonly does not extend so

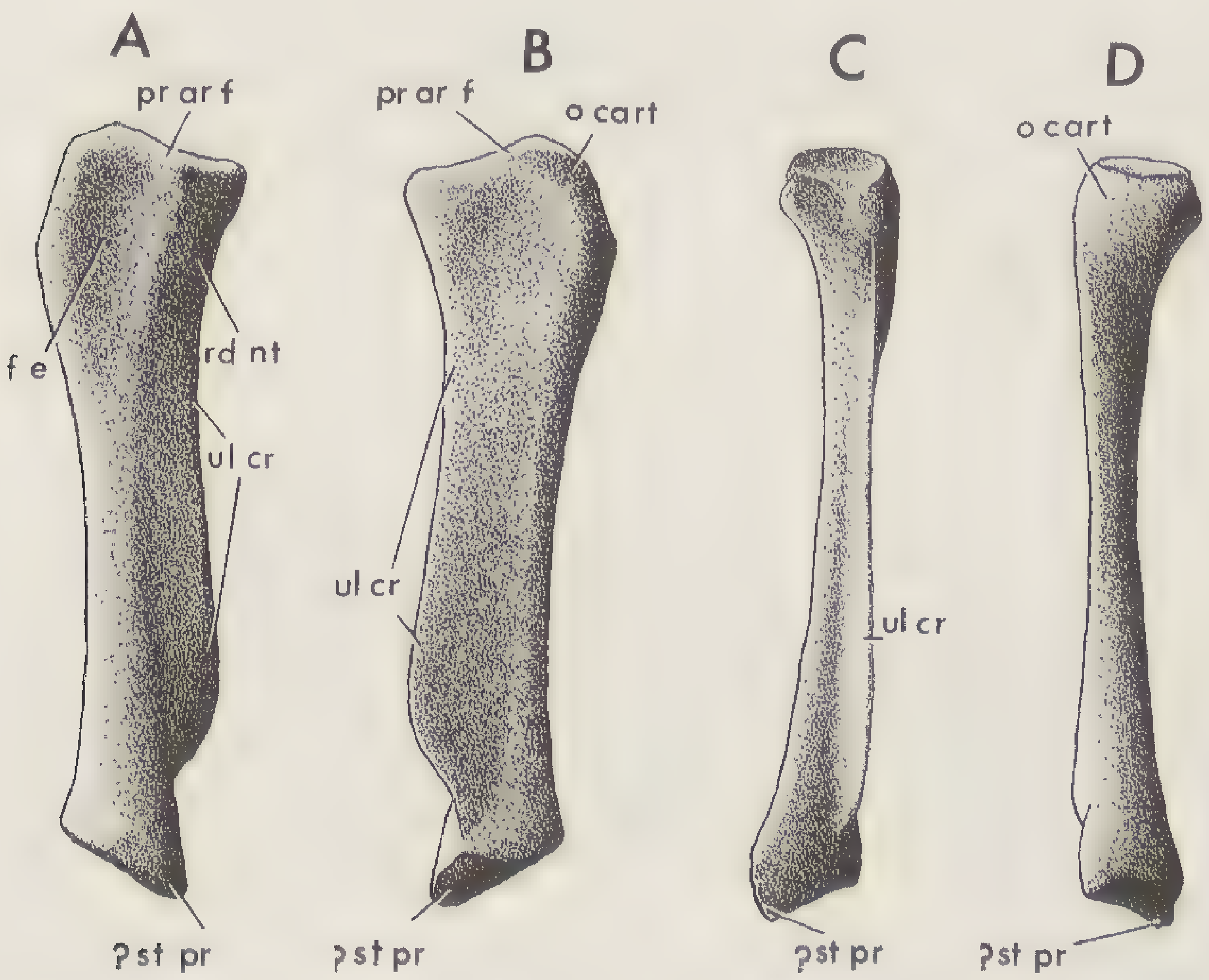

FIG. 32. Right ulna of *Thrinaxodon*, SAM K. 1395, in A, lateral; B, medial; C, anterior; D, posterior views. X1.7. Abbreviations as in FIG. 31 except: *? st pr*, styloid process questionably homologous with the styloid process found in mammals.

far distally. Its position and orientation is consonant with the interpretation that it served for the origin of an extensor muscle, possibly the M. extensor carpi ulnaris.

A high, narrow crest (*ul cr*, Figs. 31A–C, 32A–C), commencing at the anteromedial margin of the sigmoid notch, passes distally along the anteromedial aspect of the shaft. Proximally its slightly concave edge parallels the shaft axis; distally the convex edge curves medially to permit passage of the radius across the anteromedial aspect of the ulna. Haines (1946: 9) proposed that the crest (described in ?*Galesaurus* by Parrington, 1934: 60) served as the insertion for a radio-ulnar interosseous ligament. Haines' interpretation is valid although his observation that the crest was directed laterally is incorrect.

The medial surface of the ulna is smooth and almost featureless except for two confluent, shallow fossae (Fig. 31B) probably associated with the origin of deep flexor musculature. As with other features, these fossae are relatively less developed in galesaurids.

In larger cynodonts the distal articular facet is somewhat triangular in outline with a posterior "apex" and an anterior "base". The surface, bearing textural rugosity typical of the ends of cynodont limb bones, is anteroposteriorly convex. A line from the most posterior point on the surface, or "apex", to the anterolateral corner of the triangular facet follows a slight groove which describes a segment of a large circle. This line represents the anteroposterior axis of movement of the ulna on the ulnare. The distal end of galesaurid ulnae appears to be somewhat different, although in no known specimen is the end perfectly preserved. The articular area is more or less oval in outline and is set obliquely across the shaft. The anterior aspect of the facet is drawn to a blunt point (?*st pr*, Fig. 32), giving the appearance of a styloid process as in some mammalian ulnae. No trace of this feature is found in larger cynodonts.

The rim of the distal articular facet is invariably poorly preserved but in all larger specimens a tuberosity (*tb*, Fig. 31B,D) is preserved at the posterior corner ("apex") which possibly represents an insertion for a long extensor. This tuberosity is small and indistinct in galesaurids.

Manus (Figs. 33, 34A, 35)

MATERIAL. The cynodont manus is inadequately known because of poor ossification in a small number of available specimens. Only two specimens, *Thrinaxodon liorhinus* (UMC R.2733; see Parrington 1933; 1939) and *Diademodon* sp. (USNM 23352), have an apparently complete set of carpal bones, but neither is in complete articulation and the latter is poorly preserved. An acid prepared manus of *Thrinaxodon* sp. (SAM K.1395) shows details of the proximal carpals not seen elsewhere, but only seven ossicles are preserved from the (presumably) original eleven. Most of the phalanges are present.

The apparently complete and articulated carpus of *Leavachia duvenhagei* (RC 92) described by Broom (1948: 624–625) lacks the second distal carpal (Brink and Kitching, 1953a: 314).

An incomplete carpus is known for *Galesaurus* (SAM K.1119).

The specimens of *Thrinaxodon* and *Diademodon* agree with Broom's (1932b:

264) observation that *Thrinaxodon* and "a large *Cynognathus*-like cynodont" have four elements in the proximal row; radiale, intermedium, ulnare, and pisiform.

Carpus

MORPHOLOGY. The ulnare, known adequately from *Thrinaxodon* (*u*, Fig. 33) and *Galesaurus*, is the only cynodont carpal of which the orientation is certain. The galesaurid ulnare is stout, rectangular, and somewhat longer than wide, with a dorsal facet for the distal end of the ulna. The facet is saddle-shaped, the anterior and posterior halves rising only a small amount. Occupying the ventral surface is a round, shallow concavity. The dorsoventral thickness of the bone is greater medially than laterally so that in transverse cross-section the bone is triangular. The anterior face bears a flat, vertical facet for articulation with the fourth and possibly fifth (if present) distal carpal; the medial surface bears a deep groove for the reception of the intermedium. The ulnare in *Diademodon* (*u*, Fig. 34A) is transversely constricted and anteroposteriorly longer along its lateral edge than it is along its medial edge, thus differing from the rectangular shape in galesaurids. In *Leavachia* the ulnare as figured by Broom (1948: 625) is slightly constricted as in *Diademodon*, but the lateral and medial edges are subequal in length, imparting a rectangular outline as in galesaurids.

The intermedium in *Thrinaxodon* and *Galesaurus* is a flat, rectangular bone, of which one of the two longer edges is concave, the other convex. Damage and uncleared matrix on UMC R.2733 (Fig. 33) prohibits positive identification of the intermedium in this specimen, but this element is known from other specimens (SAM K.1395, SAM K.1119). The precise orientation of the intermedium is not known with certainty, but the following interpretation is most likely. The long axis is anteroposterior, with the two featureless, flat faces representing dorsal and ventral aspects. The concave (medial) long edge forms a strap-shaped facet which articulates with the rounded lateral surface of the radiale. The opposite (lateral) long edge is slightly convex and is received by a groove in the medial aspect of the ulnare. At the middle of the ventral edge of the ulnare groove is a swelling that is opposed by a slight depression on the anterolateral corner of the intermedium ventral surface. In *Diademodon* the articular relationships of the intermedium (*i*, Fig. 34A) with the radiale and ulnare are apparently the same as in galesaurids, although the bone is relatively narrower.

The radiale in *Thrinaxodon* (*r*, Fig. 33) and *Galesaurus* is a stout, oval nodule and is approximately one-third again as thick through its center than is the ulnare through its medial (thickest) edge. The dorsal surface of the radiale is a rounded facet for articulation with the radius. The medial and posterior faces of the radiale are nearly vertical. On the flat ventral surface there are two slight depressions separated by a low, oblique ridge, features which represent ligamentous or muscular attachment. The anterior face is incised with a wide, transverse groove for reception of the medial centrale. The radiale in *Diademodon* (*r*, Fig. 34A) is similar to that in galesaurids. The flat, ventral surface appears to differ in the presence of a broad groove opening onto the posterior margin and a tuberosity on the posterolateral corner. The radiale of *Leavachia* is "irregularly quadrangular" (Broom, 1948: 624), contrasting to the oval shape of later cynodonts.

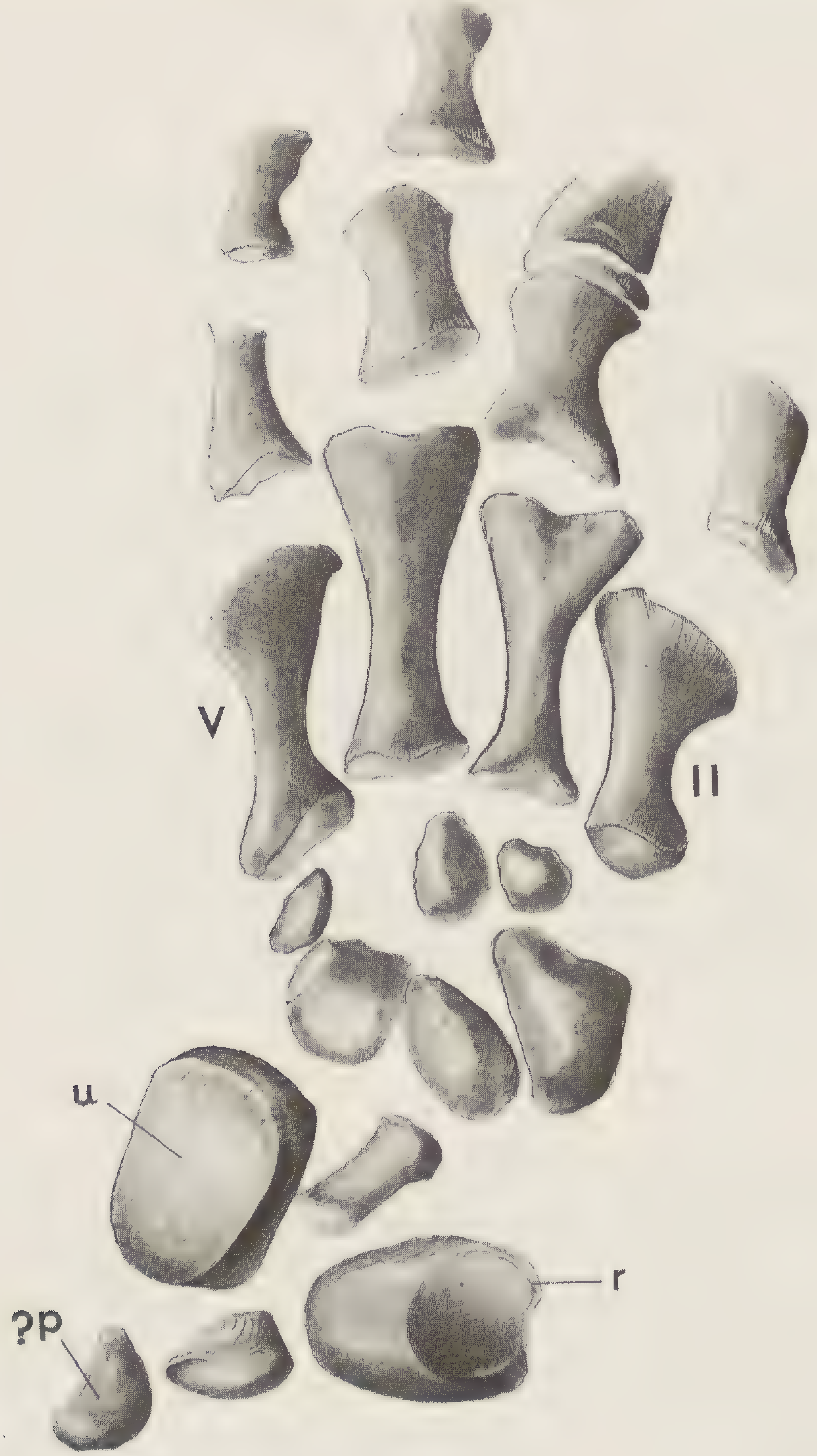

FIG. 33. Manus of *Thrinaxodon liorhinus*, UMC R. 2733, showing eleven carpals. Distal phalanges and first digit not illustrated in this view (see Parrington, 1939). Approx. X5.7. Abbreviations: *II-V*, metacarpals II-V; *?p*, pisiform, identification uncertain; *r*, radiale; *u*, ulnare.

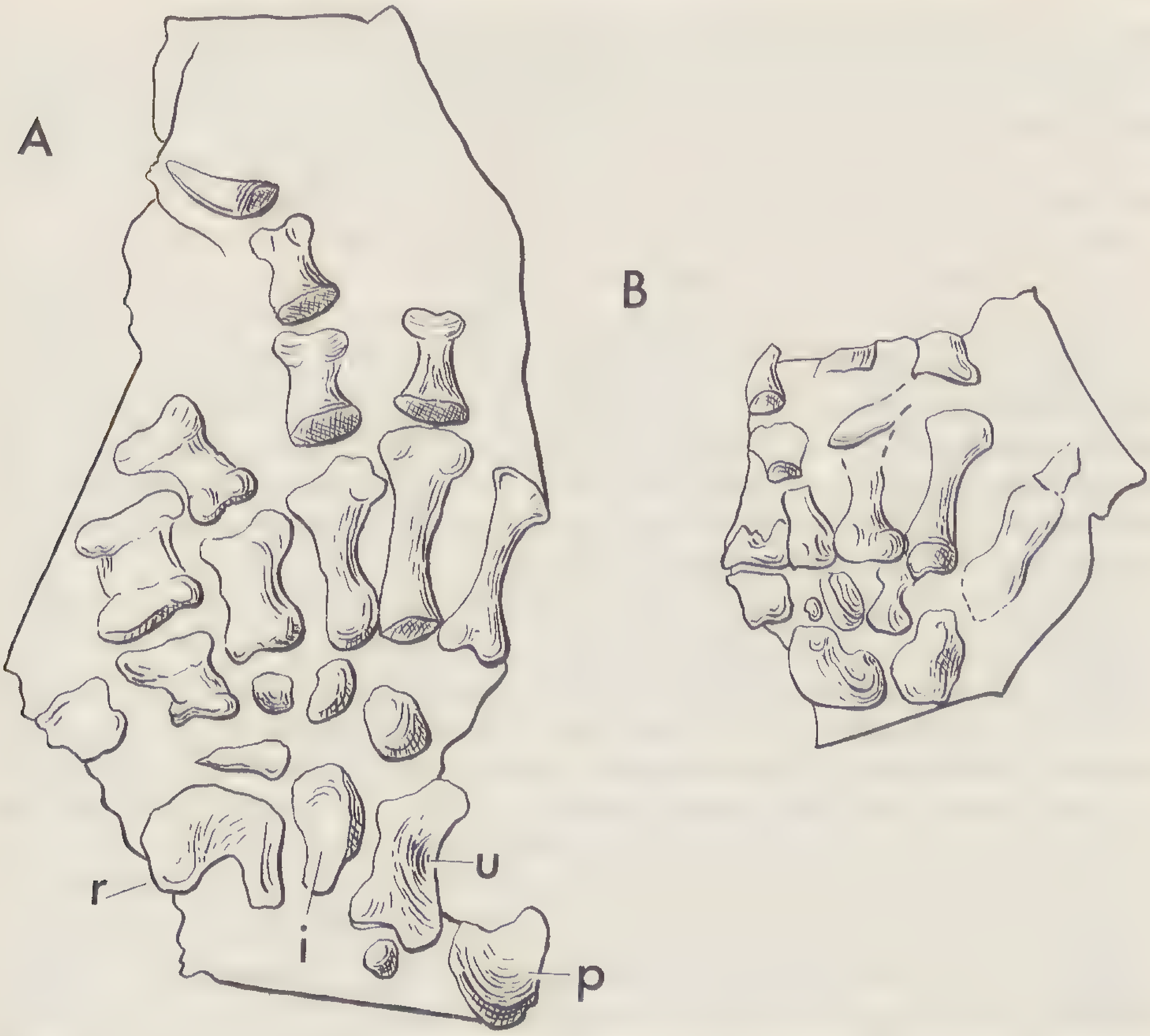

FIG. 34. A, manus and B, pes of *Diademodon* sp., USNM 23352, showing disparity in size X1.5. Abbreviations as in FIG. 33 except: *i*, intermedium.

A pisiform is known in *Thrinaxodon* (UMC R. 2733, in which the 11 carpals are disarticulated), in *Diademodon* (USNM 23352) and in *Leavachia* (RC 92). In *Thrinaxodon* the identity of the pisiform is somewhat in doubt, the probability being that it is one of the two elements preserved posterior to the ulnare (see Parrington, 1939: fig. 1). The more posterior of the two is closest to the proximolateral corner of the ulnare with which, in addition to the ulna, the pisiform typically articulates and is here considered to be the pisiform. The bone, incompletely exposed, is a flat, hemicircular disc (?*p*, Fig. 33). Although poorly preserved, the edge which Parrington (1939: fig. 2) reconstructed as straight is in fact somewhat concave and therefore the pisiform was probably crescentic in outline. In *Diademodon* (*p*, Fig. 34A) the pisiform is also crescentic but its posteromedial margin (as illustrated, not necessarily its true orientation) is swollen. As with the pisiform of *Thrinaxodon* the articular relationship of this bone remains in doubt. In *Leavachia* the pisiform is a flat, round disc (Broom, 1948: 625).

Two centralia are known to be present in the complete carpus of *Thrinaxodon* (UMC R.2733; Fig. 33) but their precise identity is uncertain because of disarticulation. An acid-prepared but incomplete carpus of *Thrinaxodon* (SAM K.1395) shows two cylindric nodules lying distal to the radiale and intermedium, with their long axes

oriented transversely to the long axis of the manus. If these are centralia, as their position would indicate, and if they are in actual articulation, then the restoration given by Parrington (1939: fig. 2), with the long axis of the lateral centrale parallel to that of the foot, is incorrect. Tentatively accepting the identification and orientation of these carpals in SAM K.1395, the following description is given. The medial and smaller of the two centralia is slightly dorsoventrally compressed. The cylindric posterior surface articulates with the transverse anterior groove of the radiale; the anterior surface bears a depression for articulation with distal carpal I. The lateral centrale is wider distoproximally and less dorsoventrally compressed than the medial, giving it a truly cylindrical appearance. In mediolateral width both centralia are equal. The only obvious articular surface on the lateral centrale is a rather vertical, round facet on its posterior aspect, evidently for articulation with the intermedium. In *Leavachia*, Brink and Kitching (1953a: 314) find that the medial centrale and radiale are fused, contrary to Broom's description (1948: 624–625).

The carpus of *Thrinaxodon liorhinus* figured diagrammatically by Broom (1932b: fig. 91) has only four distal carpalia, the fourth and fifth presumably being fused. Parrington (1933: 18–19) described and later (Parrington, 1939) figured a specimen (UMC R.2733) in which the fifth distal carpal was preserved as a small but separate element. The discrepancy between the two accounts may be tentatively settled in Parrington's favor because the specimen figured by Broom is unidentified and was later admitted to be unsatisfactorily preserved (Broom, 1936: 405). However the possibility that ossification varied with age or some other factor cannot be wholly discounted when so few determinable specimens are known. The morphological detail of the distal carpalia are not determinable from UMC R.2733 because of incomplete ossification. All are somewhat nodular and Parrington's (1939: fig. 2) assessment of their relative sizes is probably correct: I > IV > III > II > V. In *Diademodon* (Fig. 34A) there are apparently only four distal carpalia, with loss or fusion of V. All are nodular, except I which is flat and plate-like. In dorsoventral view their relative sizes are the same as in *Thrinaxodon*. In *Leavachia* also there are probably only four distal carpalia, although Brink and Kitching (1953a: 314) find that the second carpale is missing in the type specimen. There is a possibility, in view of the double facet on the distal end of the fused medial centrale and radiale, that *Leavachia* possessed only three distal carpalia, i.e., I, (II lost or fused), III, IV, (V lost or fused). Brink and Kitching's figure shows the fused centrale-radiale apparently in place and articulating with distal carpale I medially and metacarpal II laterally.

METACARPUS.

MORPHOLOGY. A complete metacarpus is adequately known in *Thrinaxodon* (BPI 376) and poorly known in *Diademodon* (USNM 23352; Fig. 34A). The metacarpals are all an elongate dumbbell shape and vary significantly only in shaft length with IV > III > V > II > I. Viewed dorsally the metacarpals appear nearly symmetrical, the proximal ends flaring laterally somewhat less than the distal ends. Viewed laterally the metacarpal outline is asymmetrical because the proximal end is much

thicker than the distal. The proximal articular facet is gently convex and rather square in outline, whereas the distal facet is flat and rectangular. A shallow depression on the proximolateral surface of all shafts except V accommodates the proximal end of the laterally adjacent metacarpal.

PHALANGES

MORPHOLOGY. Broom (1932b: 270) figured a manus of *Thrinaxodon liorhinus* as having the primitive reptilian digital formula of 2-3-4-5-3, with the second phalanx of digit III and the second and third phalanges of digit IV reduced to discs. Later Broom (1936: 405) accepted Parrington's (1933: 18–19; 1939: 211) finding that two articulated specimens (UMC R.2740) clearly had four phalanges in digits III and IV, in each case the second phalanx reduced to a plate-like disc. There is therefore no doubt that the correct digital formula for *Thrinaxodon* is 2-3-4-4-3. Considering the trend toward reduction of phalangeal number in *Lystrosaurus* zone cynodonts, it is not improbable that the larger cynodonts of the *Cynognathus* zone achieved a "mammalian" count of 2-3-3-3-3. Phalanges of both *Cynognathus* and *Diademodon* are known from two collections (BPI 1675, NMB C.2709) made from separate localities where disarticulated remains of these genera are preserved together. It is not possible, however, to distinguish morphologically two types of phalangeal elements and on the present small sample it must be concluded, barring size parameters, that homologous phalanges of these genera are identical. No disc-like, reduced phalanges were recovered in either of these collections which include many fragments as small as or smaller than the expected size for such elements. Sampling error does not account for their absence and thus there is circumstantial evidence that *Cynognathus* and *Diademodon* had a phalangeal formula of 2-3-3-3-3. The partially disarticulated manus of *Diademodon* (USMN 23352; Fig. 34A) preserves only digit III in which there are three phalanges. Crompton (1955b: 626–627) concluded that the middle Triassic cynodont *Cricodon metabolus* probably possessed a phalangeal count of 2-3-3-3-3. Thus the preponderant evidence indicates that at least several genera of advanced cynodonts had achieved a mammalian phalangeal number.

Brink and Kitching (1953a: 314) reported that the phalangeal count in *Leavachia duvenhagei* (RC 92) is 2-3-3-4-3, not 2-3-4-4-3 as Broom (1948: 626) claimed.

The detailed description of individual phalanges given below is based on the BPI 1675 collection of disarticulated, intermixed skeletons of *Cynognathus* and *Diademodon* with supplementary data from another similar collection (NMB C.2709). Not only is it impossible to separate the phalanges generically, but also there is no known feature with which to distinguish manual from pedal phalanges. The lack of variation in the known sample makes it probable that *Cynognathus* and *Diademodon* phalanges are very similar. Furthermore the manual phalanges of *Diademodon* (USNM 23352) and *Thrinaxodon* (SAM K.1395) compared to the pedal phalanges of a generically unidentifiable Middle Triassic cynodont (BMNH TR.8) show that there is little basic morphological difference between analogous fore- and hindfoot elements. Therefore until better material is available the following description applies to manual as well as to pedal phalanges.

Proximal phalanges (Fig. 35I-L) are all uniformly hourglass-shaped and approximately in the same proportions. In dorsal view (Fig. 35I) the proximal half of each expands gradually from a moderately constricted waist to a proximal terminus bearing a vertical, oval articular facet (*pr ar f*, Fig. 35L). The distal half flares abruptly to a hemispherical terminus where the crescentic, convex articular facet is inclined anteroventrally at an angle of about 45° to the long axis of the bone (*di ar f*, Fig. 35J,K).

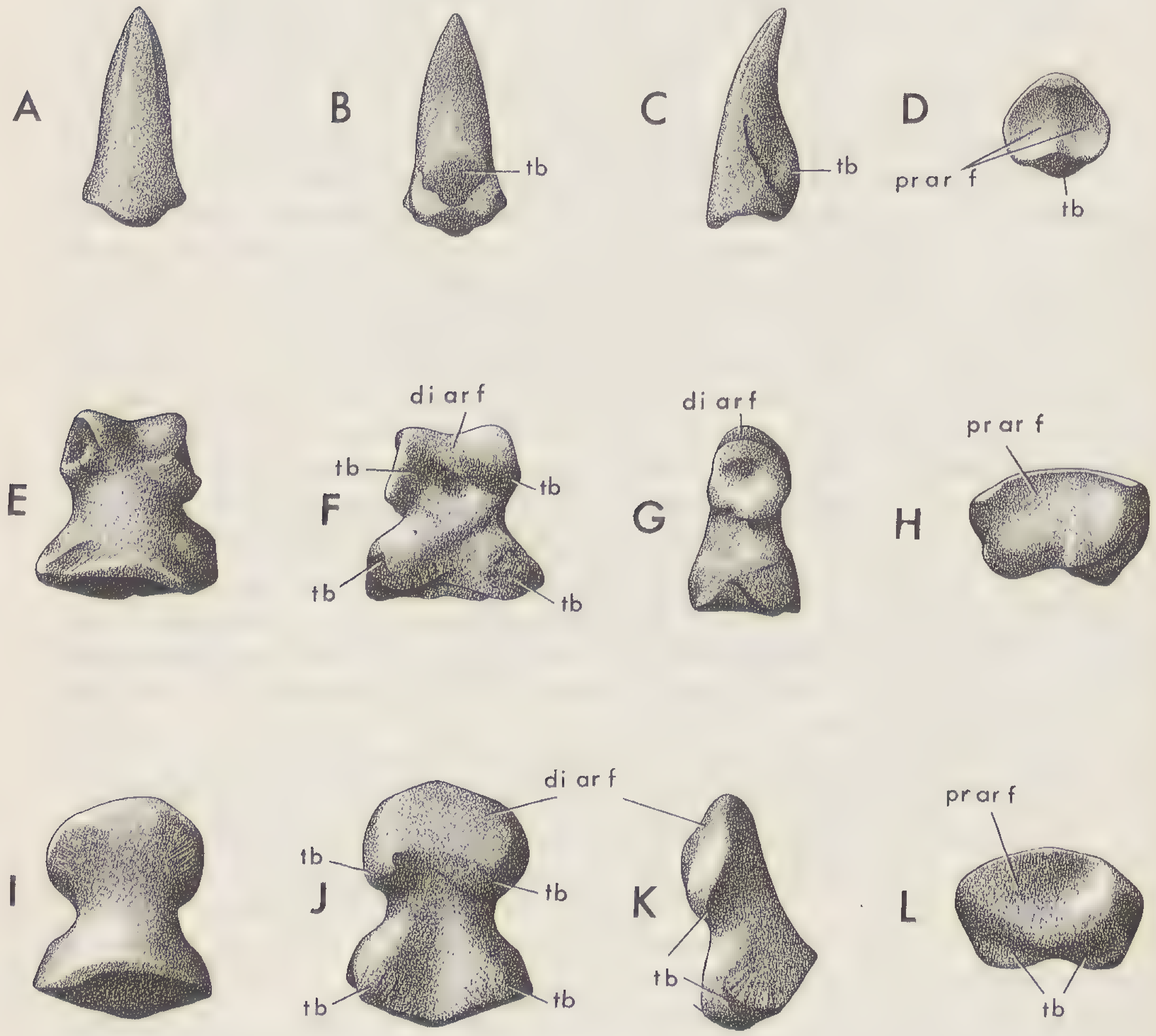

FIG. 35. Isolated phalanges of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, A–D, distal phalanx; E–H, penultimate phalanx; I–L, proximal phalanx, in (left to right) dorsal, ventral, lateral and proximal views. These elements are not necessarily from the same individual and may represent either manual or pedal phalanges, or both. X1.35. Abbreviations: *di ar f*, distal articular facet; *pr ar f*, proximal articular facet; *tb*, tubercle for ligamentous, tendinous or capsular attachment.

On the ventral surface are four tuberosities situated at the "corners" where an articular surface adjoins the ventral surface (*tb*, Fig. 35J,K); these probably functioned in attachment of ligaments or digital flexors. Striations adjoining the proximal and distal ends mark ligamentous or capsular attachments. In *Thrinaxodon* and *Galesaurus* the phalanges are longer relative to the waist diameter but are otherwise similar in morphology to those of *Cynognathus* and *Diademodon*.

Penultimate phalanges, disregarding the vestigial discs of III and IV, are also uniformly hourglass-shaped and approximately in the same proportions (Fig. 35E-H). The width of the distal terminus is somewhat less than that of the proximal. The oval proximal facet, indented along the median sagittal plane, is almost vertically oriented; it faces slightly dorsally (*pr ar f*, Fig. 35H). Articulation with the inclined distal facet of the proximal phalanx (or vestigal disc) must have normally been at an angle of about 135°. In a specimen of *Galesaurus* (SAM K.1119) two of these phalanges are preserved in articulation at an angle of 115°; however this probably represents the flexed condition common to rigor mortis. The distal end of the penultimate phalanx is essentially a cylinder, the two ends of which are concave and face slightly anterodorsally. The articular surface for the ungual phalanx is a pulley-like groove extending in an arc of almost 270°, thus permitting considerable flexion and extension of the claw (*di ar f*, Fig. 35F,G). The four corners of the ventral surface (Fig. 35F) each bear a rugose tuberosity; frequently they are asymmetric and unequal in size. The dorsal surface also bears asymmetric tuberosities at its proximal corners. The penultimate phalanges of *Thrinaxodon* and *Galesaurus* are morphologically similar to those of *Cynognathus* and *Diademodon*. Proportionally they are longer relative to their width and are thus comparatively more slender.

Cynodont ungual phalanges are slender, tapering cones with little ventral curvature (Fig. 35A-D). The distal half is somewhat dorsoventrally compressed. The articular facet is a round concavity divided sagittally by a raised median ridge (*pr ar f*, Fig. 35D) in larger cynodonts. The dorsal and ventral edges of ungual facets are extended posteriorly to form distinct lips which fit snugly into the opposing pulley-like groove of the penultimate phalanx. At the proximal base of all ungual phalanges is a tuberosity for a flexor muscle insertion (*tb*, Fig. 35B-D). There appears to be little variation among cynodont unguals, but in one complete pes (BMNH TR.8) the unguals are flatter and less pointed than in any other known unguals.

3. FUNCTIONAL CONSIDERATIONS OF THE PECTORAL GIRDLE AND FORELIMB

Introduction

The significance of the cynodont postcranial skeleton to the evolution of mammals can only be understood in functional terms. Functional analyses usually treat three different but interrelated aspects: 1) the normal position and orientation of skeletal

parts to each other, (e.g., in the case of the appendicular skeleton, the stance or habitual stationary posture); 2) the changes in position and orientation of skeletal parts during normal activity, again with respect to the appendicular skeleton, the gait or excursion of the limbs; and 3) the adaptive significance and relative efficiency of (1) and (2). If fossil material is considered, the fundamental difference between these functional aspects relates to the probability of approximating the truth in each case. For instance the stance of a fossil tetrapod is more confidently reconstructed than its gait because only basic articular relationships need be established. An interpretation of limb movement further requires evidence of muscular and ligamentous systems which often have no close analogy among living forms. The evaluation of a system's adaptive nature and relative efficiency still further requires physiological as well as paleoecological evidence which is always incomplete. Thus I regard conclusions on these three aspects with confidence decreasing (1) to (3), although I nevertheless will draw conclusions relating to each aspect.

The Shoulder Girdle of Cynodonts and the Evolution of the Mammalian Shoulder Girdle

An evaluation of the cynodont shoulder girdle in terms of the evolving mammalian shoulder girdle must take into account its basic function and mechanics. The function, of course, has remained essentially unchanged throughout tetrapod evolution: to form a stable "base" for the forelimbs which will transmit both the weight of the body and the locomotory thrust of the limbs. The mechanics of pectoral girdle function have undergone radical changes which will be discussed in this and the following section.

Romer (1922a, 1922b; see other authors cited by him) discussed the derivation of the mammalian pectoral girdle from that of primitive tetrapods. His primary concern, however, was to establish certain nervous, muscular and osteological homologies in the pectoral girdle complex of diverse living and fossil groups. Since his work, general reviews of pectoral girdle evolution have been published by Lessertisseur and Sigogneau (1965), Lessertisseur and Saban (1967) and Jouffroy and Lessertisseur (1967), but no attempt has been made to evaluate the biomechanical factors involved.

One of the fundamental problems in pectoral girdle evolution is to explain the modification of its various constituent bones in the course of the reptilian-mammalian transition. The clavicles and (posterior) coracoids are reduced in size, the latter becoming vestigial. The anterior (epi- or pro-) coracoids are, with the exception of monotremes, lost altogether. The scapulae, as Romer has shown, are remodeled by dorsal migration of musculature originally associated with the coracoid plate. The history of these complex changes is not fully known and even if it were the explanation probably would not be simple. However, as a first approximation the following analysis attempts to relate known or inferred mechanical facts to the general tendency toward pectoral girdle diminution in the ancestral mammalian lineage. The biomechanical principles employed are derived primarily from the classic work of James Gray (1944), "Studies in the mechanics of the tetrapod skeleton."

Gray (1944: 102) demonstrated that static support of the body involves employment of limbs (and girdles) as struts, whereby a limb "exerts forces along its own mechanical axis only, the moment of muscular tensions operating about the hip or shoulder joint being zero". For instance graviportal mammals are capable of aligning their limbs more or less vertically beneath the body (Fig. 36A, A′). In such a case the axial thrust of the limb due to body weight (W) is countered by an equal but opposite vertical resistance (R) at the ground. The vectorial path traveled by these forces, i.e., the mechanical axis (*MA*, Fig. 36), corresponds in this case to the morphological axis (*MOA*, Fig. 36), which is composed of the series of skeletal elements transmitting the forces. If the animal remains stationary, neither transverse or longitudinal moments of resistance are generated and the system is theoretically resolvable into a two component system of W and R. However, such simplicity of design is probably never achieved by any tetrapod because limb bones and girdles are not simple linear axes nor are the muscles and ligaments which stabilize them symmetrically arranged. Nevertheless the concept of morphological (limb) and mechanical (force) axes—the former determining the orientation of the latter—are useful in investigating relationships of limb form and function.

All tetrapod limbs are segmented and each segment is capable of variable degrees of independent position and movement. To be more precise, the morphologic axis changes course at joints. Since this is the case, transverse, longitudinal or both forces may be introduced which must be balanced by equal but opposite forces if the animal is to hold a static posture. In Figure 36B the elbow joint is bent outward in a plane perpendicular to the sagittal plane. The morphological (*MOA*) and mechanical (*MA*) axes are separated at all but two points, i.e., at the glenoid (G) and base of the foot. In such a case the transverse and vertical moments of resistance are determined from a vector analysis of the mechanical axis (*MA*). Each of the opposing forces (W, R) imparted along the mechanical axis has a vertical (Wv, Rv) and a transverse (Wt, Rt) component. For stationary stability,

$$Wt = Rt = Wv \tan a$$
$$Wv = Rv$$

where angle a is the angle between the mechanical axis and a parasagittal plane. The vertical components represent the gravitational interaction of the body weight and substrate. The horizontal component Rt represents frictional resistance of the foot applied laterally against the body. This resistance must be opposed by an equal force generated by the contralateral foot and transmitted by the body. The force opposing Rt may be regarded in terms of Wt, the resistance of the pectoral girdle and thorax to compression or, to put it differently, the competence of the pectoral girdle and thorax in transmitting the force generated by the contralateral foot. As angle a increases or decreases, so also do the horizontal components relative to vertical if equilibrium is to be maintained. An increase in the horizontal components requires structural adaptations in the shoulder girdle to resist thoracic compression and to transmit the equal but opposed forces from contralateral feet.

In Figure 36B the elbow joint is bent backward in a parasagittal plane. As in the previous case horizontal moments of W and R are introduced, but instead these act in a parasagittal and and not a transverse plane. Frictional force generated at the base

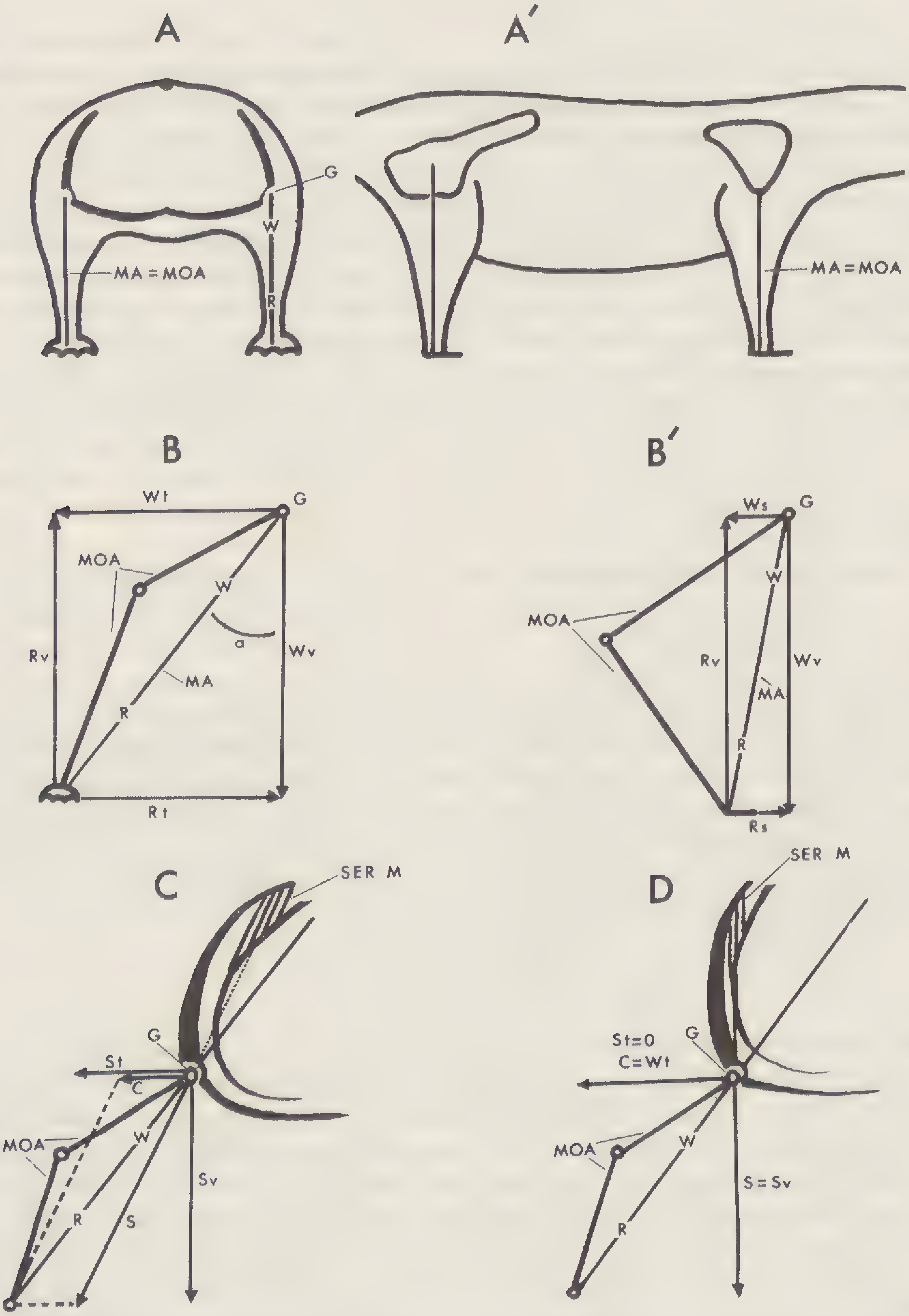

FIG. 36. Diagrammatic representation of the mechanics of tetrapod limbs, partly after Gray (1944). A, transverse section through shoulder girdle and limbs of a tetrapod. A′, parasagittal section through the same. B, B′, transverse and parasagittal sections through the shoulder girdle and forelimb of tetrapods in which the forelimb is held laterally and parasagittally, respectively. C,D, transverse sections through the shoulder and forelimb of tetrapods in which the limbs are held laterally in the same manner but in which the orientation of the scapula and serratus musculature varies. *G*, glenoid; *MA*, mechanical axis of limb; *MOA*, morphological axis of limb; *SER M*, serratus muscle. For other abbreviations and explanation, see text.

of the foot (*Rs*) is balanced by an equal but opposite force (*Ws*) at the shoulder girdle. *Ws* represents the resistivity of the shoulder girdle to independent forward displacement. Ultimately the equilibrium of the couple *Ws-Rs* depends upon an equal but reversed couple on the ipsilateral hind foot. In most tetrapods the orientation of the limb is such that both transverse (*Wt*, *Rt*) and parasagittal (*Ws*, *Rs*) components are introduced; the result is conceptually complex, but the principles involved are of course the same.

From the above examples it is sufficiently clear that limbs held away from the body axis in the so-called "sprawling position" must produce a large transverse, or compressive, component acting on the thorax. The massive, conjoined pectoral girdles of primitive tetrapods appear to have been an adaptation to sustain the compressive forces generated by sprawling limb posture. In particular the broad coracoid plate may have aided in dispersion of these forces over a relatively large area of the thorax, while the massive clavicles and interclavicle were effective transmittors of these forces to the contralateral foot. Reduction of the pectoral girdle could only follow proportional reduction of the compressive component.

In the foregoing hypothetical models the role of the scapula in transmitting forces was neglected for the sake of simplicity. Nevertheless the orientation of the scapula and other girdle elements determines to a large extent the stresses which the limbs must bear. Gray (1944: fig. 19) pointed out that the interaction of *R* and *W* at the glenoid may be analyzed in terms of the orientation of the Mm. serrati which are probably the most important muscles uniting the anterior half of the body with the scapula. His argument may be briefly restated with reference to Figure 36C, diagrammatically illustrating a transverse section of a tetrapod in which the limb is held perpendicularly to the long axis of the body. The scapular blade is inclined medially and is somewhat bowed, with the result that the Mm. serrati on the average are inclined ventrolaterally. *W* is the resultant of force *S* of the body weight transmitted to the scapula by the serratus musculature and force *C* tending to displace the scapular base laterally. The horizontal component of *S* is *St* and

$$St + C = Wt.$$

Gray did not pursue this argument to its conclusion, viz., that the transverse force *Wt* (as in Fig. 36B) is no longer wholly dependent upon the structural competence of the shoulder girdle to resist compression. The girdle is designed to generate its own laterally directed force, *St*. Limb proportion and orientation which result in larger *Rt* values may then be associated with a relatively weaker pectoral girdle. Such an arrangement seems to have been developed among the cynodonts and apparently persists in a somewhat modified form among monotremes as well. The cynodont scapula is bowed laterally to a marked degree (Figs. 17C,D; 18C,D), hence orienting the serratus musculature in the manner suggested above. Such an arrangement might have been a contributing factor in the reduction of the coracoids and clavicles from the more massive, primitive condition. The fossorial habits of monotremes and the extremely sprawling position of the humerus may have necessitated both the inclination of the scapula and the retention of the primitive, robust coracoid-clavicular complex.

Whether or not the position of the monotreme scapula is due to fossorial specialization, it remains a strong possibility that the curvature of the cynodont scapula is re-

lated to the reduction of transverse, compressive forces acting on the thorax. There is no question that the coracoid plates and clavicles are significantly reduced in size over those in pelycosaurs and early therapsids.

In Figure 36D the stance remains the same as in Figure 36C but the Mm. serrati are disposed vertically so that the horizontal component (*St*) of *S* is nil. The lateral component (*Wt*) of *W* now is accounted for only in terms of *C*, the lateral force resisting compression of the girdle. All other factors being equal between Figure 36C and D the pectoral girdle of D must have structural adaptations to resist that part of the *Rt* compressive force opposed by *St* in C. In other words the pectoral girdle of D must be stronger than that in C in order to make up for the less advantageous mechanical position of the serrati in resisting compressive forces. Such an arrangement is characteristic of pelycosaurs and other early tetrapods in which a massive shoulder girdle and vertical scapular blades are developed.

Gray (1944: fig. 19) concluded by simply noting that "if the line of action of the serratus tension does not pass through the glenoid, other external forces—active or passive—must act on the girdle in order to prevent the latter rotating inwards or outwards about the head of the humerus." If the line of action passes medial to the glenoid, as, for instance, it must in living crocodilians, the compressive effect of *Rt* is increased by *Wt*. This may be withstood by structural adaptations of the rib cage to resist deformation as well as by strengthening the shoulder girdle. This condition is not common to mammals, however, nor is the condition in which the line of serratus action passes lateral to the glenoid. In most mammals the lines of serratus action are aligned nearly vertically and scapula so closely approximates a parasagittal plane above the limb that only minor transverse forces are generated. With the exception of the condition in monotremes (see above) the mammalian coracoid plate is reduced to a small vestige for muscular attachment. The clavicles, also much reduced in size, still stabilize the scapula, as in primitive forms, but serve only a fraction of the original requirement. Thus part of the history of the mammalian pectoral girdle can be interpreted in terms of changes in forelimb position—the subject of the next section.

THE GLENO-HUMERAL ARTICULATION AND FORELIMB MOVEMENT

The mammalian glenoid is typically formed by a shallow, more or less circular glenoid cavity which faces ventrally. The cavity is surrounded by a fibrocartilaginous glenoid labrum which somewhat deepens the cavity, forming a rounded socket for reception of the humeral head. In primitive tetrapods the glenoid was neither circular nor ventrally facing, but had a peculiar, twisted morphology, best described as screw-shaped, and faced laterally. The derivation of the mammalian pattern involved not only major morphological modifications but also postural and functional changes as well. In order to evaluate cynodonts as an intermediate stage the primitive arrangement, i.e., in pelycosaurs, must be fully understood.

PELYCOSAURS

The screw-shaped glenoid common among Paleozoic tetrapods has been discussed

by Watson (1917a), Romer (1922b), Miner (1925) and Haines (1952), each of whom supposed that its intricate morphology permitted accurate reconstruction of humeral movement. Nevertheless there is surprisingly little agreement among these authors on movements of the humerus. No evaluation of the functional advantage of a screw-shaped glenoid has even been given. Yet the persistence of this structure among pelycosaurs and primitive therapsids (Deinocephalia) renders it fundamentally important to the understanding of synapsid forelimb evolution. The morphology of the forelimb and pectoral girdle of the Pelycosauria, thoroughly documented by Romer and Price (1940), will not be redescribed here except where required to clarify functional analysis. *Dimetrodon* may be taken as representing a primitive synapsid condition; the small amount of morphological variation in the forelimb skeleton of pelycosaurs makes it unnecessary to consider other forms. Before presenting my conclusions concerning the early evolution of the glenoid and forelimb movement, the contributions of previous authors will be considered.

Watson (1917a: 13 ff.) attempted to reconstruct *Dimetrodon* forelimb mechanics on the basis of articular relationships and inferred musculature. He concluded that the humerus, held at right angles to the sagittal plane, lay nearly parallel to the ground, that it could not have been advanced much beyond the right angle position, but that it could have been retracted posteriorly as much as 50°. Watson estimated that in "normal position" (normal stance?) the antebrachium would lie at a 30° angle to the ground. He further concluded that the antebrachium was restricted in transverse movement, i.e., movement parallel to a vertical plane through the humeral axis, by the deep sigmoid notch of the ulna, but that a limited amount of anteroposterior movement was made possible by "the spheroidal shape of the ulnar articulation." In Figure 37 a *Dimetrodon* right forelimb and pectoral girdle are diagrammatically illustrated to show phases of the locomotory cycle as interpreted from Watson's (1917a) description. In Figure 37 (A, A′, A″) the humerus is parallel to the ground and at right angles to the body; the forearm is at an angle of 30° to the ground and essentially parallel to the body. From this position the humerus is retracted and slightly depressed and the elbow is flexed to give a position as in Figure 37 (B, B′, B″). Simultaneously the humerus is rotated on its long axis (depressing the anterior and elevating the posterior aspects of the bone) to permit elevation of the antebrachium. The combined action of these movements advances the pectoral girdle, but at the same time moves it dorsolaterally toward the foot. Figure 37 (C, C′, C″) and (D, D′, D″) depict the completion of the cycle whereby "the whole anterior part of the body is . . . swung from side to side at each stride."

Romer (1922b: 548–550) also recognized that humeral action in primitive tetrapods required, in addition to the principal anteroposterior movement, abduction and adduction (raising and lowering) as well as long axis rotation. However he objected to Watson's apparent assumption that the screw-shaped glenoid represents a single articular facet. Romer pointed out that the opposing facets would therefore represent segments of rather large circles and that "any motion of more than 20° would cause the humerus to cut the muscular surfaces at the anterior and posterior edges of the joint." He furthermore concluded that such an arrangement would generate excessive friction. Instead, Romer proposed that both humeral head and glenoid bore two "partially separated" facets, one anterior and one posterior (see also Romer and Price,

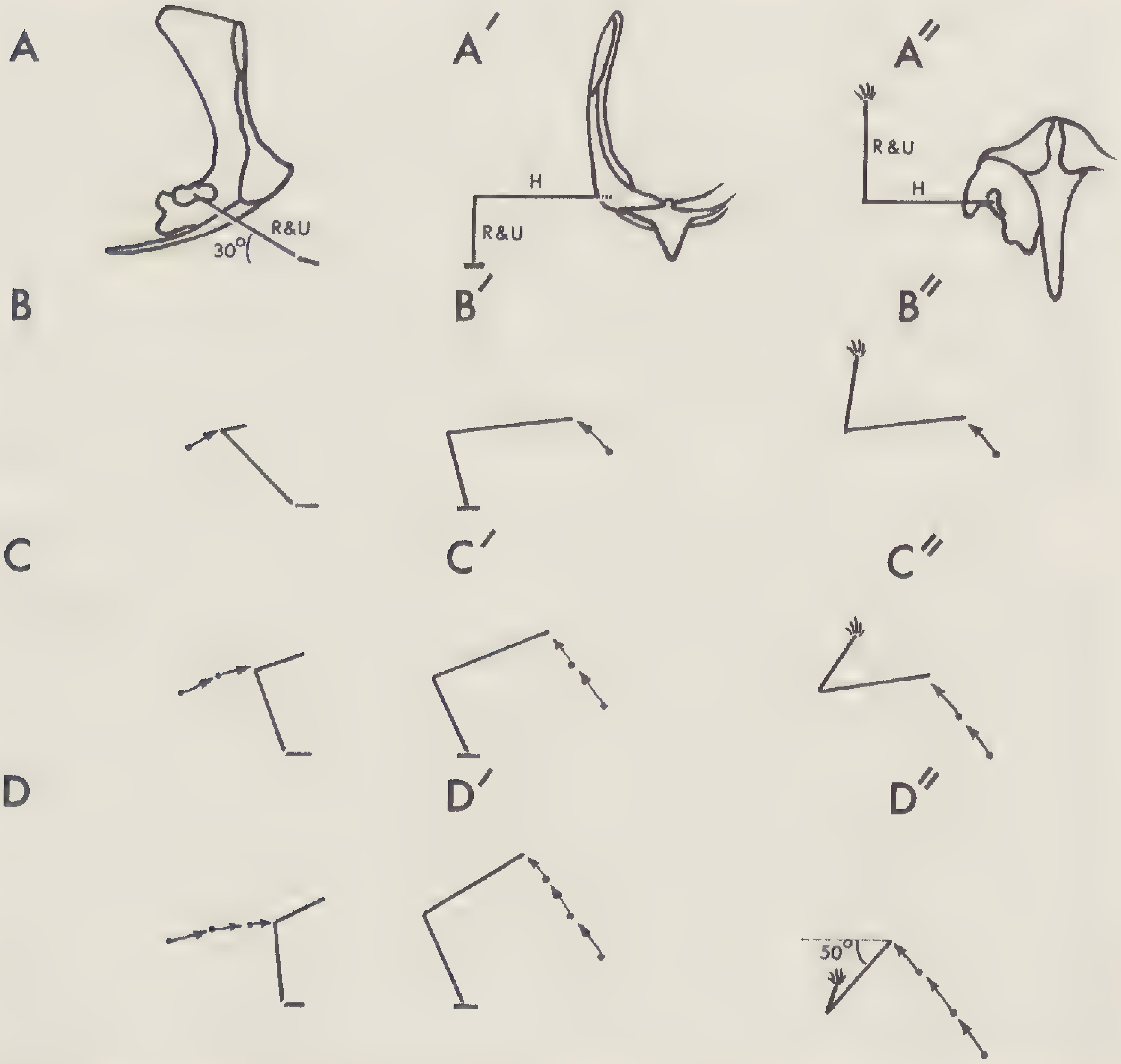

FIG. 37. Diagrammatic representation of forelimb movement in *Dimetrodon* as proposed by Watson (1917a). From left to right: lateral, anterior and ventral views. A, A′, A″ represent the start of the propulsive stroke; D, D′, D″ the completion of the propulsive stroke. *H*, humerus; *R & U*, radius and ulna.

1940: 138). His evidence for such a division—a slight ridge on some humeri and a contraction in the outline of the glenoid—is dubious at face value and since no functional explanation is given, the concept renders the screw-shaped glenoid even more enigmatic. Moreover two separate surfaces, as proposed by Romer, would virtually prohibit any movement but simple abduction and adduction. Anteroposterior movement is prohibited by the interference of adjacent facets. I conclude from an examination of well-preserved humeri and glenoids that there is no reliable evidence of separate facets and that, as will be shown in detail below, the complex morphology of the screw-shaped glenoid and spiral humeral head are related to diverse functional requirements of a single articular joint.

Miner (1925: 165–168) described in detail the glenohumeral articulation in *Eryops*. According to his interpretation the humeral head articulates with the posteriorly facing, anterior half of the glenoid when the humerus is in its posterior position

at the end of the propulsive stroke. As the humerus is brought forward again, the head slides posteriorly along the glenoid surface and reaches the dorsolaterally facing, posterior half of the glenoid at the completion of the recovery stroke. In addition to the sliding action of the joint Miner claimed that humeral movement entails a long axis rotation of about 90°. Watson (1917a: 3) had previously denied the possibility of long axis rotation in *Eryops*. He interpreted the screw-shaped glenoid and humeral head as fitting so snugly that humeral movement was restricted to a small amount of anteroposterior movement with a minor dorsoventral component. However Watson's description did not take into account the cartilage that undoubtedly covered both surfaces during life; such a cartilaginous cap would in effect separate the apparently interlocking bony surfaces. Therefore accepting Miner's view, longitudinal rotation of the humerus is part of primitive forelimb function.

Finally Haines (1952: 419–421) attempted to reconstruct the movements of the humerus in *Dimetrodon* taking into consideration the action of supposed cruciate ligaments. A dorsal and a ventral pair of these ligaments, arranged in an "X" pattern across the glenohumeral articulation, are common among living lizards. Haines concluded that movement of the distal end of the humerus "followed a roughly circular track" similar to that exhibited by lizards and urodeles. However Haines did not work with any fossil material, his conclusions on *Dimetrodon* being based on a paper and paste model constructed from published figures. Therefore it is difficult to accept his contention that two such utterly disparate glenohumeral joint types as that of *Dimetrodon* and modern lizards should be functionally the same. In fact there is no osteological evidence that pelycosaurs possessed cruciate ligaments, but even supposing they did, Haines admits that "slight changes in the lengths or positions of these ligaments may make great differences in the movements." While cruciate ligaments are critical regulators of humeral movement in the relatively simple "ball and socket" type joint of some living reptiles, the pelycosaurian shoulder mechanism is at least partly defined by the intricate morphology of the glenoid—irrespective of the accessory support of ligaments and glenoid capsule.

My conclusions on pelycosaur forelimb mechanics are based primarily on an unusually well-preserved scapulocoracoid and humerus of an adult *Dimetrodon* sp. (MCZ 3357) from the Belle Plains Formation of Texas. Unlike much pelycosaur material the bone is undistorted and preserves detailed textural features. Morphological details were verified insofar as possible in other specimens (MCZ 2951 and YPM 661 in particular).

The glenoid in *Dimetrodon* is about 15 to 20 percent shorter anteroposteriorly than the humeral head facet. In MCZ 3357, for instance, the glenoid is 61 mm long and the humeral head 73 mm; there is no reason to interpret the glenoid as having been longer by virtue of cartilaginous overgrowth without also supposing the humeral head was likewise increased in length. The fact that the humeral facet is longer anteroposteriorly than the glenoid facet is prima facie evidence for anteroposterior movement of the humerus along an essentially horizontal track as postulated by Watson. Such a movement could not have taken place by means other than a sliding of the respective articular surfaces on one another, the mechanism proposed by Miner for *Eryops*. According to this view the anterior end of the humeral facet passes beyond the anterior limit of the glenoid as the humerus is retracted; conversely, as the humerus is brought for-

ward, the posterior end of the humeral facet passes beyond the posterior limit of the glenoid. Romer (1922b: 549) claimed that such facet displacement would sever adjacent muscular and ligamentous tissues and entail excessive friction as well. But Miner (1925: 167–168) correctly pointed out that among living tetrapods the surface area of the humeral head is usually larger than that of the glenoid socket. The displacement of part of the humeral articular facet from the glenoid surface follows the obvious principle of any "ball-and-socket" type joint. In living tetrapods, and presumably in fossil forms as well, the articular capsule and adjacent musculature are arranged so as not to be strained during normal movements.

Watson (1917a) correctly surmised that the propulsive and recovery strokes of the humerus in *Dimetrodon* involve more than simple anteroposterior swing, although he failed to present any morphological evidence for his rather specific conclusions. During the propulsive stroke depression (or adduction) and long axis rotation occurs. Evidence for such movements is derived from the reorientation of articular contacts which must occur if the humerus is to preserve the sliding articulation previously shown to be necessary. Since the changing interrelationships are conceptually complex to present, attention will be focused initially on the anterior aspects of the humeral head and glenoid.

The anterior quarter of the glenoid faces primarily posteriorly, but also slightly laterally and, if the scapular orientations given by Romer and Price, 1940, are correct, ventrally. The surface bears a low convexity (*glen convex*, Fig. 38) which falls away in all directions except posteroventrally where it tapers to a gradually attenuating ridge (*r*, Fig. 38). The corresponding anterior quarter of the humeral head is slightly concave and faces dorsomedially. This concavity (*hum concav*, Fig. 38) is continued as a very shallow groove (*hum gr*, Fig. 38) posteroventrally along the ventral margin of the facet. When the humerus is in its most anterior position the glenoid convexity and humeral concavity fit together; the latter is so oriented that in order to key with the former the distal end of the humerus must be slightly elevated (relative to the proximal end) and its distal ventral surface brought to face anteroventrally. In such a position the antebrachium is directed anteriorly to begin the propulsive stroke (Fig. 39A). As the humerus is retracted the glenoid convexity (together with its posteroventral ridge) loses contact with the humeral concavity but follows, as on a track, the groove extending posteroventrally along the humeral head. In other words the humeral concavity leaves the glenoid convexity by sliding forward as the distal end of the humerus moves back. But the proximal end of the humerus cannot slide directly forward without the glenoid convexity encountering a similar convexity on the humerus (*hum convex*, Fig. 38). The path of least resistance, therefore, lies along the shallow groove which winds posteroventrally around the head to reach the ventral surface of the humeral head. In order for the glenoid convexity to follow this groove, the humerus must be rotated anteroventrally and at the same time depressed. The rotation causes the distal, ventral surface of the humerus, which at the beginning of the stroke faces anteroventrally, now to turn ventrally, permitting elevation of the antebrachium (Fig. 39B).

At the completion of the stroke the most ventral sector of the humeral groove abuts against the glenoid convexity. The humeral concavity is displaced anteroventrally and is out of contact with the glenoid.

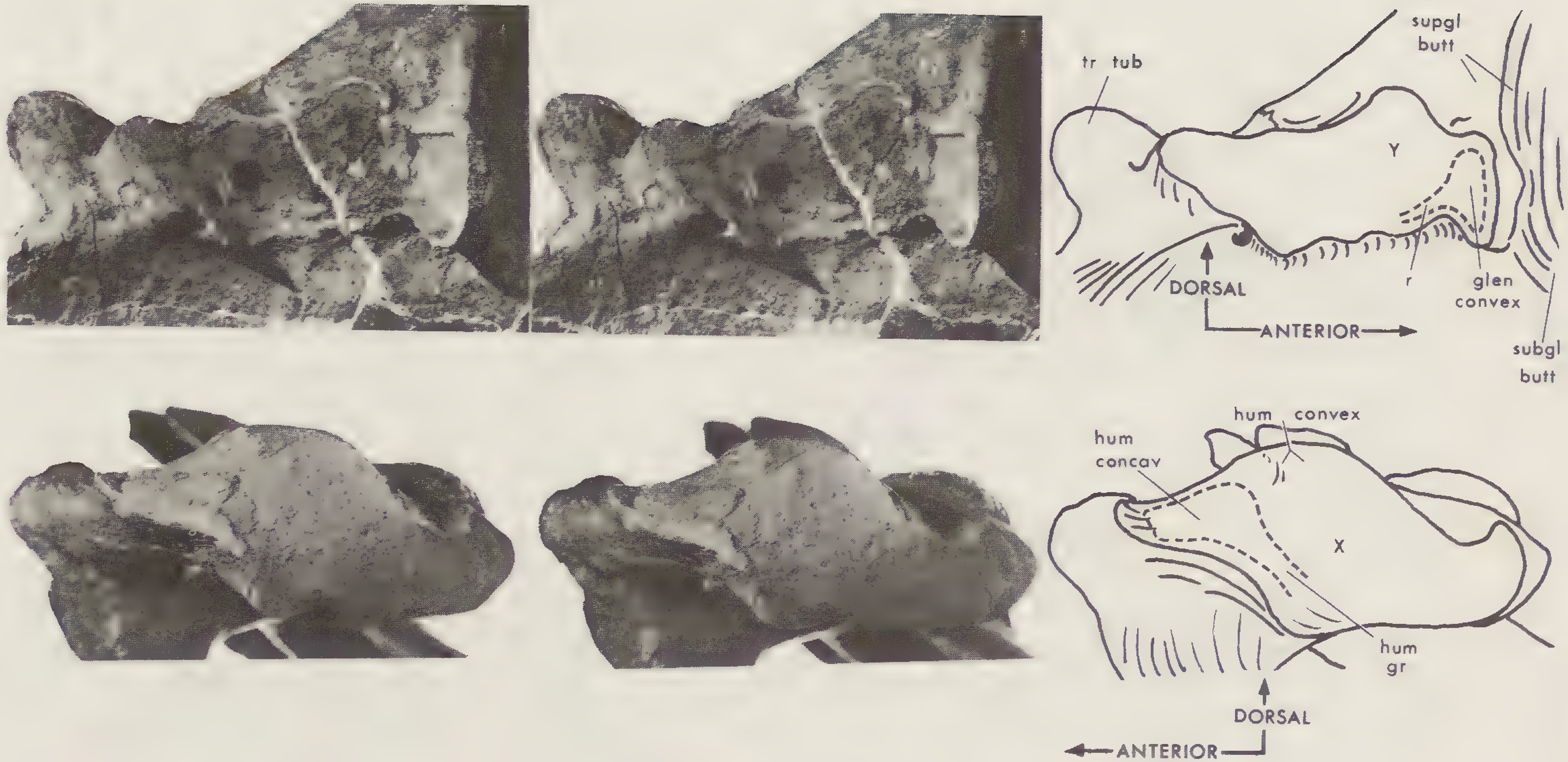

FIG. 38. Stereoscopic photographs of the glenoid (top) and proximal end of the humerus (bottom) of *Dimetrodon sp.* MCZ 3357. X0.7. Abbreviations: *glen convex,* glenoid convexity; *hum concav,* humeral concavity; *hum convex,* humeral convexity; *hum gr,* humeral groove; *r,* ridge; *subgl butt,* subglenoid buttress; *supgl butt,* supraglenoid buttress; *tr tub,* tubercle for the coracoid head of the triceps; *X, Y,* points of contact during the final stage of the propulsive phase.

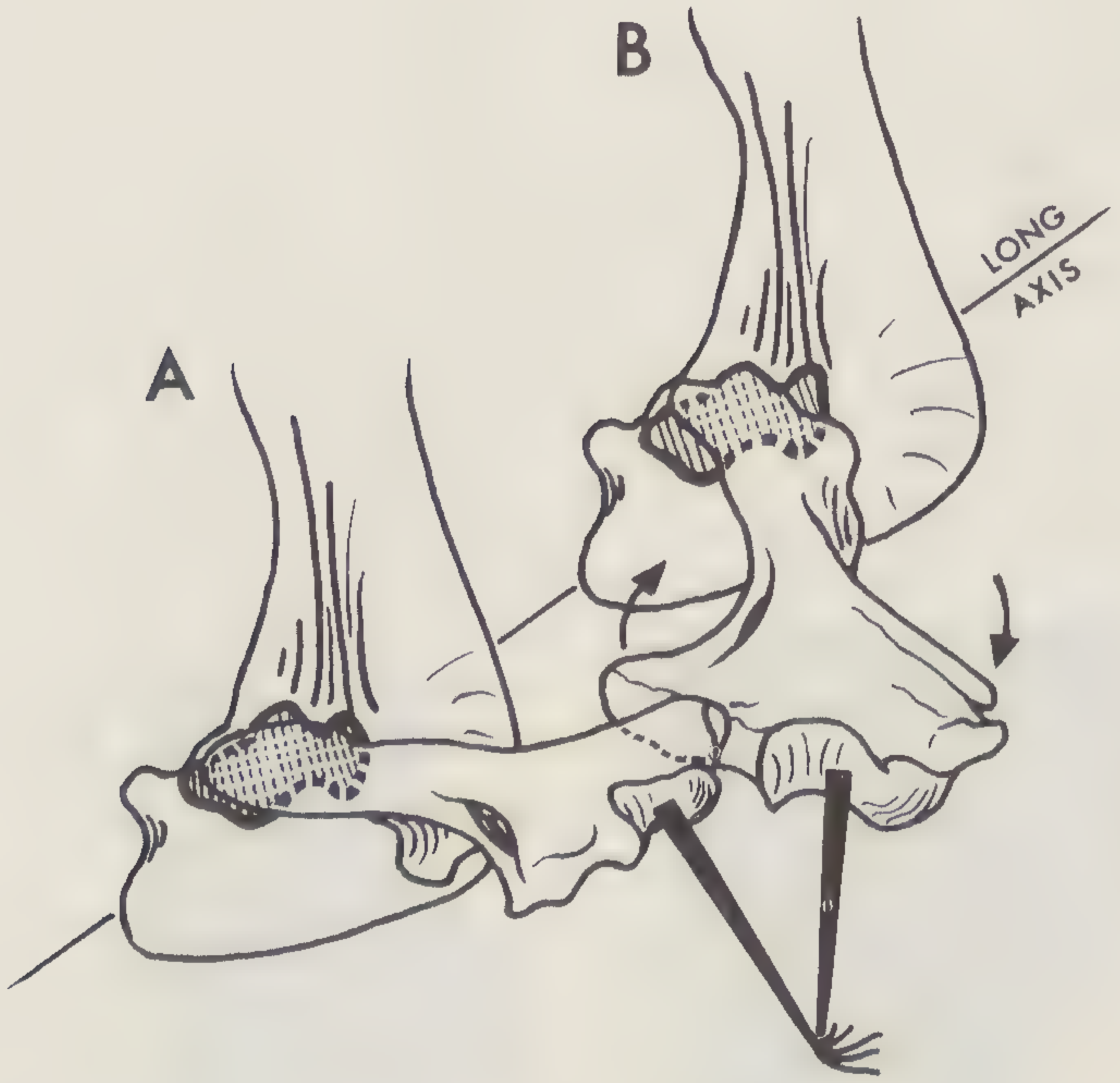

FIG. 39. Diagrammatic reconstruction of the scapulocoracoid and forelimb of a walking pelycosaur viewed from the posterolateral aspect. A, the beginning of the propulsive phase, with the antebrachium directed forward; B, the completion of the propulsive phase, with the humerus rotated (arrows) on its longitudinal axis to permit elevation of the antebrachium. *Long axis,* longitudinal axis of the body.

The remainder of the glenoid and humeral head facets are constructed to facilitate the humeral movements described above. The posterior half of the glenoid is a broad shelf which faces dorsolaterally and slightly anteriorly (Fig. 38). This half merges with the anterior half of the glenoid across a surface which is nearly vertical and faces laterally and, more anteriorly, posterolaterally. The posterior half of the humeral head is a strap-shaped surface, convex both dorsoventrally and anteroposteriorly (Fig. 38). This surface, facing medially and slightly ventrally, contacts the posterior half of the glenoid at the beginning of the stroke. Since the humeral surface does not face so much ventrally as does the glenoid surface dorsally, the humerus must be slightly elevated for the two surfaces to make even contact. At the completion of the stroke the posterior sector of the strap-shaped humeral facet is rotated dorsally out of contact with the glenoid. Simultaneously the anterior sector of the strap-shaped surface (*X*, Fig. 38) is brought into contact with the center sector of the glenoid (*Y*). This brings the

broadest surface of the humeral head into contact with the most strongly buttressed part of the glenoid during the completion of the propulsive phase when propulsive forces are maximal.

Mechanically the screw-shaped design of the primitive glenoid served two functions in early tetrapod terrestrial locomotion: longitudinal rotation of the humerus and distribution of propulsive forces. The adaptive significance of a screw-shaped glenoid with respect to humeral rotation and propulsive forces will be evaluated separately.

Longitudinal rotation of the humerus, as Romer (1922b: 548) suggested, is required to preserve the humero-antebrachial articulation during locomotion. Among primitive tetrapods flexion and extension permit independent movement of the antebrachium relative to the humerus in a transverse plane, but the nature of the primitive trochleo-capitular joint conjoins the humerus and antebrachium in any movement in a parasagittal plane. Thus as the humerus moves from a position behind the antebrachium (at the beginning of a stroke, see Fig. 37A″) to a position more or less on line with the antebrachium (at the end of a stroke, see Fig. 37D″), the capitulum, for instance, must rotate from an anteriorly directed to a ventrally directed position. The persistence of the screw-shaped glenoid in face of the obvious alternative of a simple ball-and-socket joint, eventually evolved independently by reptiles and mammals alike, might be explained by its functional advantage to a system in which neuromuscular control for terrestrial locomotion was only primitively developed. The screw-shaped glenoid and spiral humeral head provide set trackways, so to speak, along which the joint must function. Minimal muscular coordination of complex simultaneous movements is required because the articulation effectively controls abduction or adduction as well as rotation once an anterior or posterior movement is initiated. Thus it appears that a possible lack of advanced neuromuscular coordination in the forelimb of primitive forms is compensated by the restrictive control of a specialized joint.

The glenoid of all tetrapods in addition to transmitting a portion of the weight to the forefoot must transmit to the body the propulsive forces generated by the limb. Propulsive forces are of course primarily anteriorly directed, although there is some reason to believe, following Watson (1917a: 14) and the functional analysis given above, that early tetrapods had a considerable transverse component as well. A glenoid formed on a laterally directed scapulocoracoid plate, as is the primitive pattern, is poorly suited to transmit forward propulsive forces to the body. Without structural adaptations to contain the propulsive force of the limb the resulting tendency would be to disarticulate the humeral head in an anterior direction. The screw-shaped glenoid accommodates the anterior propulsive force by means of its posteriorly directed anterior half (Fig. 38). The fact that the center of the glenoid faces as much laterally as posteriorly, in addition to the fact that there is a slight lateral inclination in the anterior half, probably reflects the presence of a substantial transverse component in the stroke as postulated above. These forces are further distributed to the scapulocoracoid via structural buttresses which reinforce the anterior half of the glenoid. The supraglenoid buttress (*supgl butt*, Fig. 38) is a thickened wedge of bone passing anterodorsally from the glenoid to the scapular blade. A similar feature, the subglenoid buttress (*subgl butt*, Fig. 38), passes anteroventrally to the procoracoid plate. Both structures reinforce that part of the glenoid receiving the main propulsive force or, in other words, distribute this force over the greater part of the pectoral girdle.

CYNODONTS

The cynodont shoulder girdle bears major structural changes from the pelycosaurian pattern that are indicative of a more functionally mammalian locomotor system. The most important changes involve reduction of the coracoid plates and modification of the glenoid. Vestiges of the pelycosaurian grade remain, however, such as the tuberosity for the triceps' coracoid head and the robust clavicles and interclavicle, and thus the cynodont shoulder girdle is a mosaic of advanced and primitive features. Few major changes are evident in the humerus and antebrachium which tend to be more conservative elements in early locomotor evolution. The most important modification of the humerus is in the loss of the spirally shaped head; in the antebrachium, the most salient characteristic is the increased robustness of both radius and ulna. A functional interpretation of the cynodont forelimb and girdle will be given after an evaluation of previous work.

Glenoid orientation and humeral position

Watson (1917a: 27–30) reconstructed the girdle orientation and limb action of a cynognathid, utilizing disarticulated and unassociated remains. He concluded that the shoulder girdle was inclined forward as in the echidna; that the glenoid cavity faces "outwards and backwards"; and that the humerus "normally" was carried parallel to the ground. There are inconsistencies to such conclusions and unfortunately Watson did not clarify his reconstruction by illustration. The cynodont scapula unquestionably does incline anteriorly, for in a vertical or posteriorly inclined position the procoracoid assumes an improbable position dorsal to the coracoid (also see Broom, 1948: 623). The question, therefore, concerns the degree of anterior inclination which in turn determines the glenoid orientation and consequently the humerus orientation. If the procoracoid-coracoid ventral margin is taken as parallel to the midventral line, as Watson seems to have implied, then the scapula inclines sharply forward (Fig. 40A). In such a position the glenoid is oriented posterolaterally, as Watson claimed, but also faces somewhat dorsally which clearly was not Watson's intention because the humerus must then be slightly elevated. Alternatively if the ventral margin of the coracoid plate is slightly elevated anteriorly and also turned medially to conform with the shape of the thorax, the glenoid faces posterolaterally but also somewhat ventrally (Fig. 40C). Watson did not account for the necessary ventral component of glenoid orientation because he apparently overlooked the ventral bowing in the proximal end of the humerus (see above, p. 113). If the humerus is articulated with a more or less horizontally facing glenoid, the ventral bowing would elevate the elbow above the glenoid level (Fig. 40B). This arrangement is very improbable because the antebrachium, articulating at right angles to the distal end of the humerus, would be forced into the strenuous position of an inclined, lateral strut (*dotted line*, Fig. 40B). In addition the loss of net length to the limb would elevate the body only a short distance from the ground. Alternatively if the glenoid is oriented to face slightly ven-

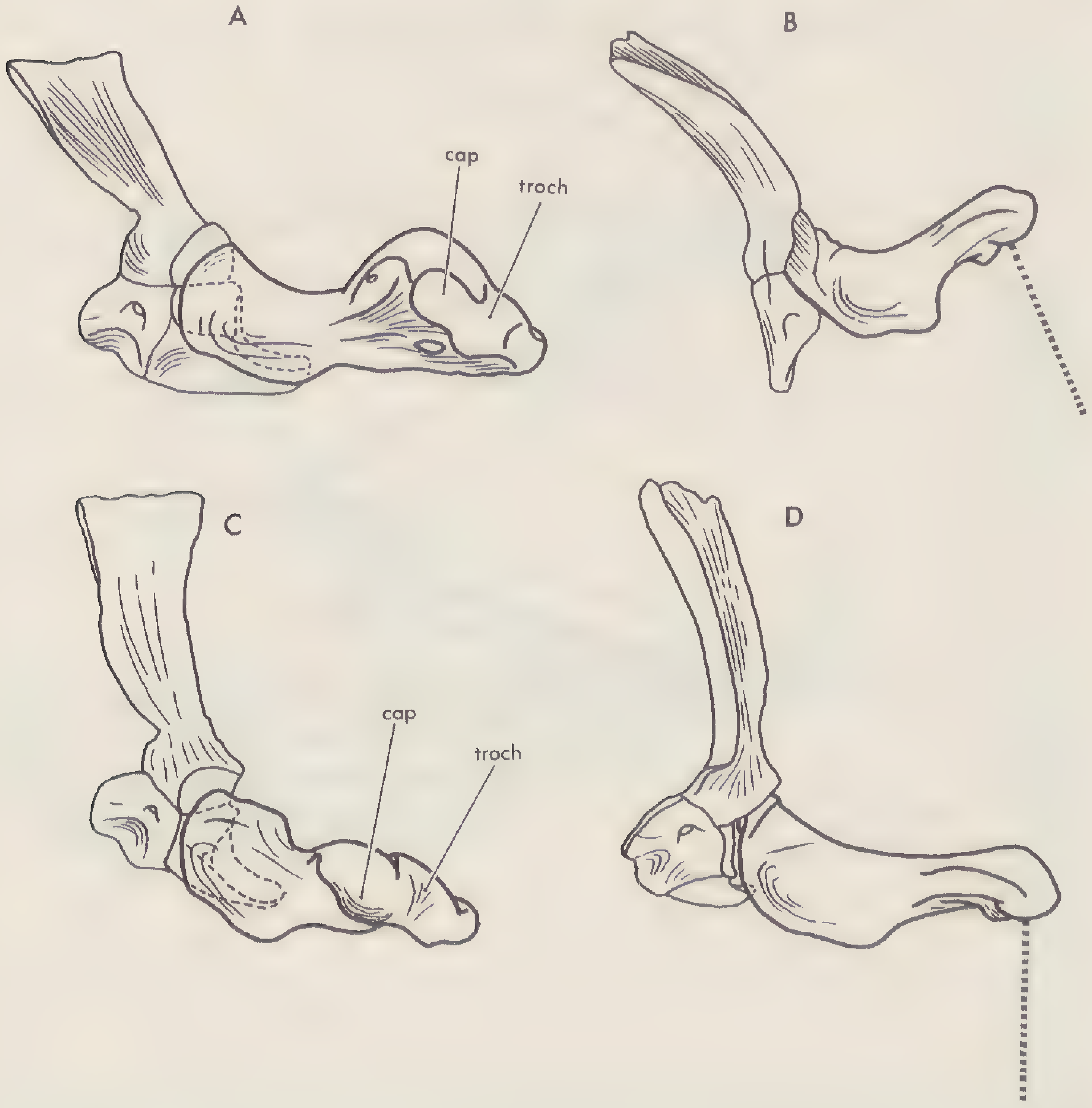

FIG. 40. A, lateral; B, anterior views of a cynodont scapulocoracoid and humerus to show the orientation of these bones as interpreted by Watson (1917a). C, lateral; D, anterior views of the same illustrating the present interpretation. *Dashed line,* antebrachial axis; *cap,* capitulum; *troch,* trochlea.

trally, the proximal end of the humerus rises dorsally to meet the glenoid and the distal end is depressed slightly below the glenoid level. The bowed relationship of the proximal and distal ends of the humerus further requires that the ventral edge of the coracoid plate be directed somewhat medially. If the coracoid plate is oriented vertically, as permitted by Watson (Fig. 40B), the humerus must orient in the glenoid in such a way that the capitulum and ventral part of the trochlea face ventrolaterally (Fig. 40A) instead of ventrally as required by a normal relationship with the antebrachium (Fig. 40D).

Correcting the foregoing inconsistencies in Watson's orientation of the scapulocoracoid and humerus a more realistic interpretation may be summarized as follows: lateral aspect of coracoid plate facing ventrolaterally as well as slightly anteriorly to conform with thoracic curvature; scapular blade inclining approximately 25° ante-

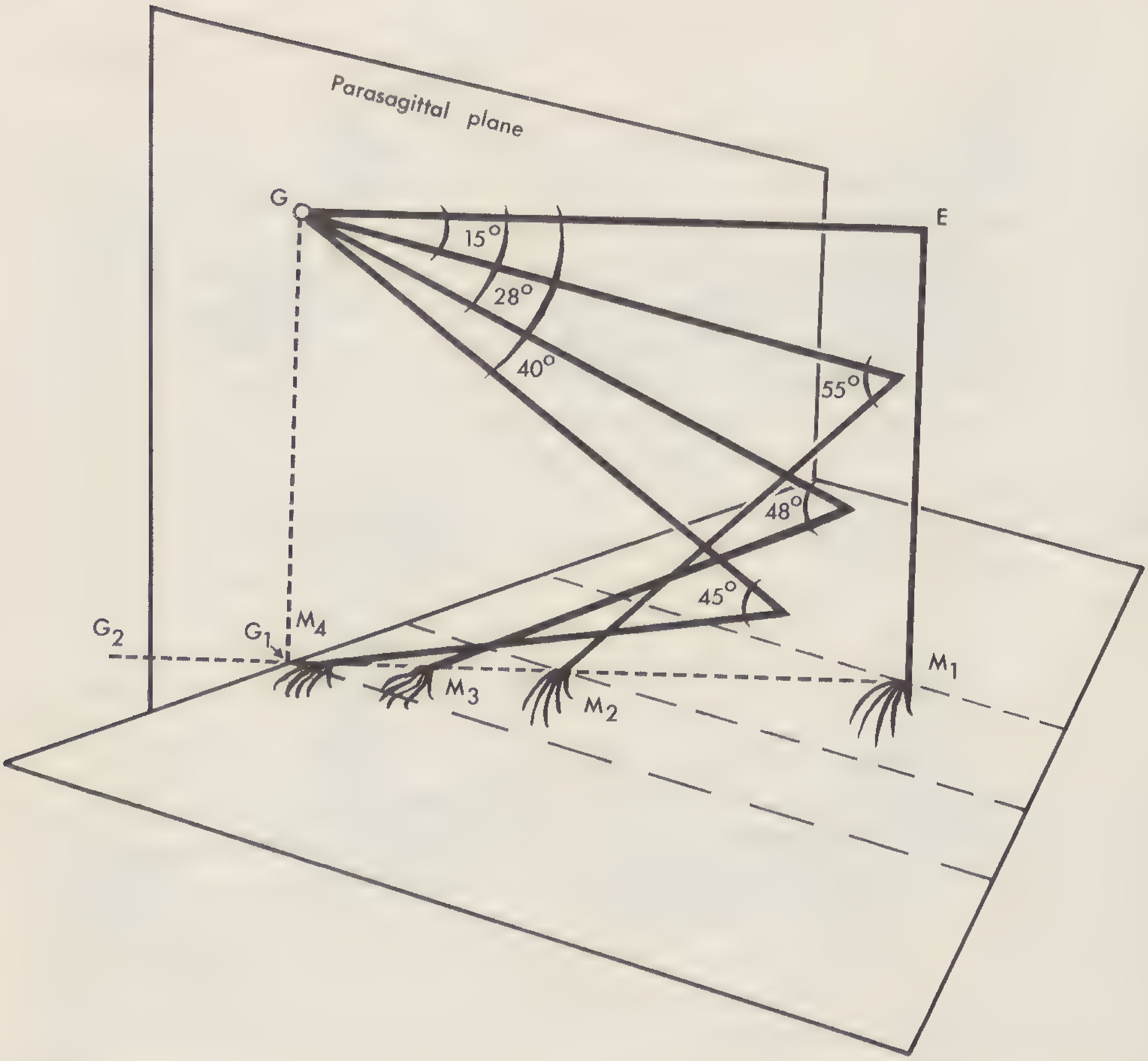

FIG. 41. Diagrammatic representation of the mechanics of cynodont forelimb movement which follows from Watson's (1917a) interpretation. Watson believed that the cynodont forelimb moved primarily in a plane (G, E, M_1, G_1) at 45° to a parasagittal plane as here represented. See text for further explanation.

riorly; glenoid facing posterolaterally as well as slightly ventrally; long axis of humerus at an angle of 45° to sagittal plane; distal end of the humerus somewhat lower than the glenoid and with the capitular surface directed more or less ventrally.

Gregory and Camp (1918) were the first to make direct comparisons between the cynodont and monotreme shoulder girdle and humerus; their restoration of *Cynognathus* forelimb and shoulder musculature implied that cynodonts had achieved a basically "prototherian" grade of organization in this respect. Yet these authors explicitly stated that the shoulder girdle in *Cynognathus* is "almost intermediate between *Sphenodon* and monotremes" insofar as both primitive reptilian and mammalian features are represented. Nevertheless the numerous, and rather superficial, points of comparison that Gregory and Camp drew between the shoulder girdle in monotremes and cynodonts invites the conclusion that monotreme anatomy represents a primitive structural stage of mammalian evolution toward which cynodonts were progressing.

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Replacement pages for pages 147-154, Yale University Peabody Museum of Natural History Bulletin 36 (1971), The Postcranial Skeleton of African Cynodonts, by Farish A. Jenkins, Jr.

Certainly the cynodont shoulder girdle already possessed certain features which monotremes retain, e.g., the eversion of the cranial border, or scapular spine, and morphology and orientation of the coracoids. However it is more accurate to classify these features as pertaining to a cynodont rather than a prototherian level of organization because monotremes have evolved distinct postcranial specializations of their own. These specializations, primarily associated with a fossorial habitus, invalidate the assumption that monotremes represent a general prototype of primitive mammalian structure and function. Howell (1936: 425) wrote that "with few exceptions (as Ribbing) most of those who have worked with monotremes have implied that they are among the most primitive mammals in their myological arrangement, as well as in general features. On the contrary, their musculature is so extremely specialized that it is very misleading to use this order for illustrating early steps in the phylogeny of mammalian myology." Howell's opinion is perhaps as extreme as the view that he rejects. The truth of the matter lies in between, namely, that features of the monotreme postcranial musculoskeletal anatomy must be evaluated individually, for some are recognizable correlates of a fossorial habitus while others reflect a primitive heritage.

Glenoid orientation and humeral position are among the most obvious features in monotremes which might be compared with cynodonts. Superficially, at least, the rounded notch of the monotreme glenoid resembles the cynodont glenoid cavity; both are formed by the scapula and coracoid, a small part of the procoracoid contributing in cynodonts. The humeri of both show many morphological similarities. However certain important details of this comparison reveal that there are basic differences in the orientation of the glenoid and humerus. First, there are significant differences in the orientation of the glenoid within the Monotremata. In *Tachyglossus* the glenoid faces laterally and somewhat ventrally, whereas in *Ornithorhynchus* it faces posterolaterally and somewhat dorsally. If monotremes are primitive, which is the primitive orientation? In cynodonts, of course, the glenoid is interpreted as having faced posterolaterally and ventrally, an orientation not apparently represented among monotremes. As for the position of the humerus, an examination of monotreme skeletal material, both articulated and disarticulated specimens, shows that the distal end of the humerus is held at a higher level than the proximal end—a feature developed in parallel among the fossorial Insectivora. Correlated with this is a typically long antebrachium which is, in *Tachyglossus* and *Ornithorhynchus* at least, 100 percent or slightly more of the humeral length. A relatively elongate antebrachium is perhaps a response to the height lost due to the repositioning of the humerus subsequent to fossorial adaptation. Some of the reasons why such a posture was probably not characteristic of cynodonts are discussed above with reference to Watson's (1917a) paper. The distal end of the cynodont humerus appears to have been normally positioned below the level of the glenoid, a fact clearly depicted by Gregory and Camp's (1918: Pl. XLI) comparative illustration of *Cynognathus* and *Ornithorhynchus*. Furthermore, the cynodont antebrachium is known to be on the order of only 75 percent of the humeral length (see below). If the cynodont humerus assumed a monotreme posture the forelimb would not be long enough to maintain the trunk well off the ground during locomotion.

Monotremes do not appear to represent a reliable model on which to base interpretations of the cynodont glenoid and humeral orientation. Further functional and

comparative anatomical studies on the Prototheria may provide a sound basis for discriminating habitus from heritage features in these and other characters. At the present time, however, one must regard the cynodont, not the monotreme, as representing the primitive, "prototherian" pattern.

Locomotion

Watson (1917a: 29–30) made deductions concerning the locomotory function of the cynodont forelimb. He believed that excursion of the humerus was limited to depression and elevation along a vertical track, with no anteroposterior movement of the distal end. The forefoot is placed on the ground ahead of and medial to the glenoid by fully depressing the humerus. From such a position the humerus is elevated and the antebrachium extended, driving the glenoid over the forefoot. At this stage the antebrachium continues extension but the humerus is depressed, thus moving the glenoid in front of the forefoot to complete the stroke. In this interpretation Watson overlooked several important anatomical features and also apparently was not aware of some awkward biomechanical implications that his theory of forelimb function entailed. First, Watson admitted to not having seen any cynodont radius or ulna; these are now known from an associated skeleton of *Diademodon* sp. (USNM 23352) to be on the order of 75 per cent of humeral length. The relative shortness of the antebrachium, therefore, makes it improbable that the foot could have been placed much in advance of the glenoid in the manner Watson proposed. In Figure 41 the forelimb of *Diademodon* is drawn diagrammatically to scale. The view is perpendicular to a plane with corners at the glenoid (G), the elbow joint (E), the manus (M_1), and a point below the glenoid (G_1). Watson claimed that the forelimb must act along this plane which lies at 45° to the sagittal plane. In his view the manus must fall at some point along the line M_1-G_2. In order for the manus to reach a point just short of the glenoid (M_4) the humerus must depress 40° and the antebrachium must be flexed on the humerus at least 45°. However the articular facets involved do not permit this much depression or flexion. The abrupt ventral termination of the humeral head by the bicipital groove leaves little or no facet surface to contact the glenoid when the humerus is depressed by 40°. It is even less likely that the antebrachium could have been flexed within 45° of the humerus since no part of the trochlea or capitulum faces sufficiently proximally. In order for the manus to reach a point (G_2) beyond the glenoid, which Watson claimed was the case for cynodonts and probably occurs in all tetrapods, the amount of flexion and humeral depression reaches impossible limits.

Another factor that casts doubt on Watson's interpretation is the amount of lateral movement that would be generated. At each stride, no matter what the length, the shoulder girdle, and consequently the body, would be moved as much toward the contralateral side as forward. The greater the stride along the line M_1-G_1 the more the body is displaced contralaterally during the propulsive phase. Such a locomotory mechanism would be extremely clumsy and strenuous and has no analogy among any living or fossil tetrapod. If the stride is shortened to M_3, for instance, excessive flexion of the forearm is still required and the contralateral displacement is almost as great as for M_4. At position M_2 the degree of depression and flexion are within possible limits

but the stride length is shortened to about one-half the humeral length—extremely inefficient and unlikely for the predaceous animals that some cynodonts were.

Watson (1917a: 27) claimed that "the cylindrical shape of the humeral articulation shows that the bone can have had freedom of motion only in the vertical plane". Cylindrical is an apt but incomplete description of the cynodont humeral head in which maximum curvature is dorsoventral. Depending upon the preservation there is also mediolateral curvature (Fig. 27A), and thereby the head approximates the spherical condition of mammalian humeral heads. The cynodont glenoid does not closely match the form of the humeral head (cf. Figs. 21 and 27A) although the articular cartilage probably formed somewhat more congruent surfaces. The scapular and coracoid halves of the glenoid are not smoothly confluent to form a cylindrical cavity but have an angular contact along the scapulocoracoid joint. The glenoid is therefore notch-like (Fig. 21). This distinct angulation gives the appearance of functionally discrete surfaces, a possibility that will be discussed below. Contrary to Watson's claim both the scapular and coracoid surfaces of the glenoid are not flat, for the latter in particular shows anteroposterior curvature. Moreover, the anterolateral (or external) margin of the glenoid consistently extends so far anteriorly in relation to the rest of the margin that the glenoid outline is asymmetrical; the most anterior part of the glenoid faces directly laterally in contrast to the remainder of the cavity which is oriented posterolaterally (Fig. 21). The glenoid is therefore not a close fitting counterpart to the humeral head but bears irregularities which must be interpreted in terms of greater freedom of humeral movement than Watson allowed.

The following interpretation of cynodont forelimb mechanics takes into account the range of movements which appear morphologically possible and which relate to the basic pattern developed among earlier synapsids. Pelycosaur humeri swung anteroposteriorly, but in doing so were adducted (depressed) or abducted (elevated) and rotated along their long axes. It is very likely that cynodont humeri had a similar pattern of movement because osteologically and therefore presumably myologically (as will be shown below) they are not far removed from the pelycosaur condition. However, unlike that in pelycosaurs the cynodont glenohumeral articulation does not restrict humeral positions. The recovery stroke probably involved abduction (elevation) of the humerus, as it does in most tetrapods, as well as anterior movement and longitudinal rotation of the humerus. The glenohumeral articulation obviously permits abduction, as Watson noted, and the anterolateral extension of the glenoid allows the humerus to swing anteriorly. There is no direct evidence for longitudinal rotation of the humerus, although a rotation of about 30° appears theoretically possible for this joint type. However in view of the increase in stride distance made possible by humeral rotation it is likely that the cynodonts, like their pelycosaur ancestors, preserved this functionally advantageous component in forelimb movement. As the humerus is brought forward and rotated clockwise (Fig. 42A–C) the lesser tuberosity tends to contact the posteromedial surface of the coracoid half of the glenoid; the slight recess (*Rec*, Fig. 21) in the glenoid surface at this point may have accommodated the incursion of this structure.

During the propulsive phase (Fig. 42D,E) the humerus is retracted posteriorly with respect to the glenoid and at the same time is depressed and rotated. The rota-

FIG. 42. Interpretation of the movement of a cynodont forelimb during locomotion, as seen in lateral view. A, stationary position; B, initial forward movement of limb: humerus elevated and rotated (clockwise on left side), antebrachium flexed; C, forelimb positioned for initial propulsion: humerus depressed, rotation continued from B, maximum antebrachial flexion; D, propulsive phase: humerus depressed and rotated (counterclockwise on left side), antebrachium extending; E, completion of propulsive phase: humerus maximally depressed, rotation completed, antebrachium extended.

tion permits the antebrachium which is anteroventrally directed at the beginning of the stroke to be elevated vertically and thus drive the humerus forward. The antebrachium which is probably flexed during recovery is extended on the humerus during the propulsive phase.

The angular relationship of the coracoid and scapular halves of the glenoid cited above as possible evidence for a functional division in the glenoid may be analyzed in terms of recovery and propulsive phases in forelimb movement. In the recovery phase the distal end of the humerus is elevated (Fig. 42A–C); simultaneously the head is depressed and contacts the lower (coracoid) half of the glenoid (*a*, Fig. 21). This surface is convex but slopes primarily anteroventrally. The humeral head, also being convex, makes minimal contact (which reduces friction) and is easily moved anteroventrally (*b*, Fig. 21). In this position both proximal and distal ends of the humerus are anteriorly situated for the beginning of the propulsive stroke (Fig. 42C). As the distal end of the humerus is depressed at the beginning of the propulsive phase (Fig. 42D) the head is raised and gains contact with the scapular half of the glenoid (*c*, Fig. 21). This half of the glenoid, facing posteroventrally and somewhat laterally, receives the thrust of the propulsive stroke which is directed anterodorsally and somewhat medially. The glenoid arrangement in cynodonts is therefore analogous to that in pelycosaurs with the anterior or scapular glenoid receiving the propulsive thrust and the posterior or coracoid glenoid elevating the humerus in the recovery phase. The scapular glenoid is stoutly built around the base of the scapular blade to withstand propulsive stress and to transmit body weight to the humerus.

From the position illustrated in Figure 42C, the propulsive stroke is completed by extension of the elbow joint coupled with a slight counter-clockwise (seen from the left) rotation of the humerus (Fig. 42D,E). These actions elevate the body and move it forward.

In terms of forelimb movements cynodonts probably did not depart from the basic pelycosaurian locomotory pattern although loss of the screw-shaped glenoid permitted greater freedom of movement. However, the orientation and relationship of cynodont shoulder girdle and limb elements are so much modified that despite a primitive pattern of limb movement the resulting mechanical system is well advanced toward a mammalian condition. The following are major functional differences between pelycosaurs and cynodonts with regard to the forelimb and girdle:

1) In cynodonts the glenoid is formed by contributions from the scapula, coracoid and procoracoid as in pelycosaurs, but the procoracoid contribution is extremely small. The monotreme procoracoid is excluded from the glenoid. In terms of the composition of the glenoid, pelycosaurs, cynodonts and monotremes form a morphogenic series. However the monotreme glenoid is otherwise quite specialized in orientation (see above) and morphology. Shaped as a crescentic, symmetric notch, the monotreme glenoid is of a pattern similar to that found among modern lacertilians. In cross-section the glenoid is C-shaped with dorsal and ventral aspects of the cavity smoothly confluent. In cynodonts the glenoid is asymmetric, the largest part being borne by the scapula. The asymmetry is in part related to differentiation of discrete functional areas of the glenoid (see above), a trend already begun in pelycosaurs and in other primitive tetrapods. Functional differentiation of the cynodont glenoid especially with

regard to the nearly circular and slightly concave scapular part presages the development of the mammalian scapular glenoid.

2) In cynodonts the scapular glenoid which receives the propulsive thrust faces posteroventrally and slightly laterally whereas in pelycosaurs the analogous surface faces posterolaterally and very slightly, if at all, ventrally. The obvious difference in cynodonts is the reduction of the lateral component in propulsion which does not contribute to forward locomotion.

3) As a corollary to (2) the component of forward thrust in cynodonts is more closely aligned with the long axis of the scapular blade than it is in pelycosaurs. Since the resistance to forward thrust, in terms of body weight, is in large part transmitted via the scapula, propulsive forces which do not act in close opposition to the main axis of the scapula tend to produce torque. Among pelycosaurs the gravitational force of body weight borne by the scapula passes in a ventral direction through the glenoid but the force due to propulsive thrust passes anteromedially through the glenoid; the resulting torque tends to rotate the anterior border of scapulocoracoid medially. This torque is obviously resisted by the robust clavicles and interclavicle. In cynodonts the propulsive thrust is against the scapular base and is directed anterodorsally and only slightly medially. The direction of such force accounts for the anterior inclination as well as the medial curvature of the scapular blade which is reoriented so that both gravitational and propulsive forces are transmitted more in line with its own axis. This represents an initial stage in the trend toward a mammalian scapula which alone (or with a much reduced clavicle) transmits forces between body and humerus.

4) In pelycosaurs the long axis of the humerus, from head to trochlea, is straight and in average position is horizontal. In cynodonts the proximal half of the long axis is bowed ventrally so that in average position the humerus is depressed below the glenoid level. A less horizontally oriented humerus is an important stage in the reduction of medially directed forces which necessitate the primitive, "braced" type of shoulder girdle. A more vertically oriented humerus transmits proportionally greater propulsive forces directly to the scapula.

5) The inferred arrangement of scapulocoracoid musculature in cynodonts, although scarcely mammalian in plan, represents an advanced stage in an evolutionary trend established in the stegocephalian-cotylosaurian-pelycosaurian grades. The importance of medial curvature in the scapular blade to the reorientation of serratus musculature has been shown above (see p. 135); by reducing the role of the pectoral girdle in resisting compressive (transverse) forces the pectoral girdle loses its structural massiveness and gains the potential of participating in forelimb movement as in mammals. Other apparent trends in muscular displacement relate primarily to the origins of humeral rotators which appear to have become arranged for more efficient and perhaps rapid rotation. In addition the tendency to increase the area of attachment of humeral adductor muscles is evidence that these may have increased in size, functional importance or both.

In primitive tetrapods the M. subcoracoscapularis, originating on the dorsomedial

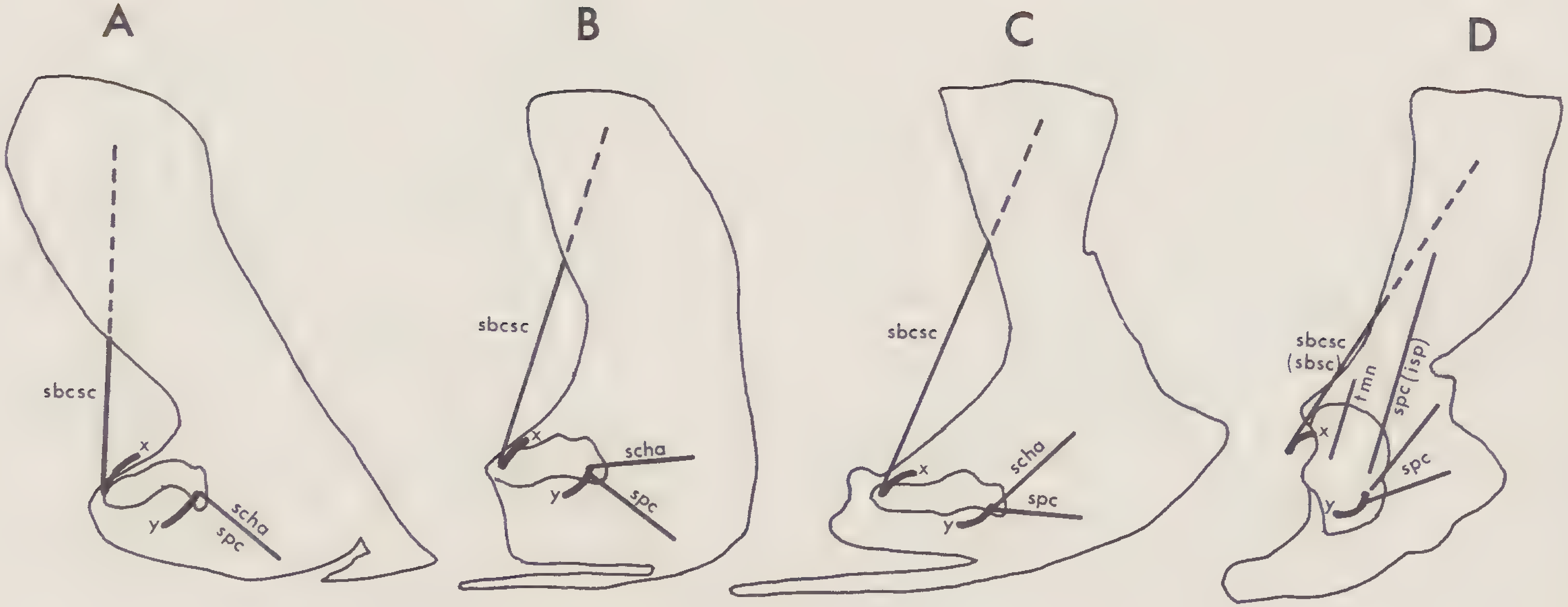

FIG. 43. Diagrammatic representations of the scapulocoracoid plate and reconstructed muscle actions in A, *Eryops; B, Diadectes; C, Dimetrodon; D, Cynognathus. x,* position of the insertion of subcoracoscapularis musculature at the completion of the propulsive phase; *y,* the same for supracoracoideus musculature. Other abbreviations as in FIG. 19.

surface of the scapula and inserting on the proximointernal angle of the humerus, analogous to a lesser tuberosity, elevated the posteror aspect of the humerus. This movement, assisted by the guiding "trackway" of the screw-shaped glenoid, brought about an anteroventral rotation of the humerus during the propulsive stroke. In *Eryops* (Fig. 43A) the traction of the subcoracoscapularis is directly dorsal or perhaps slightly posterodorsal. The arc of movement described by the point of insertion is a segment of a relatively large circle, and thus the total longitudinal rotation of the humerus is small per unit of muscular contraction. In *Diadectes* and *Dimetrodon* (Fig. 43B,C) the scapular blade is displaced anteriorly relative to the glenoid and so also is the origin of the subcoracoscapularis relative to its insertion. The inferred traction is anterodorsally directed, slightly more in *Dimetrodon* than in *Diadectes*, and thus rotation of the point of insertion (to *x*) is greater per unit of muscular contraction. In other words, the arc described by the rotation of the subcoracoscapularis insertion is a segment of a relatively smaller circle than in *Eryops*, with the consequent possibility of more rapid movement. In cynodonts (Fig. 43D) this trend is carried still further. The foregoing analysis is not an estimate of the amount of anteroventral rotation but only the relative efficiency with which this rotation was accomplished. In *Eryops* longitudinal rotation was perhaps as much as 90° (Miner, 1925: 167) but in cynodonts it could not have been more than 30°.

The Mm. scapulohumeralis anterior and supracoracoideus of primitive tetrapods opposed the subcoracoscapularis by effecting reverse rotation as the humerus was brought forward during the recovery stroke. In *Eryops* (Fig. 43A) these muscles probably took origin ventrally on the procoracoid in a position anteroventral to their insertion on the proximoexternal angle of the humerus (analogous to a greater tuberosity). When the humerus had completed the anteroventral rotation of the propulsive stroke these muscles effected a posterodorsal counter-rotation starting from point *y*. This rotation took place along a broad arc which is a segment of a relatively large circle. In *Diadectes* and *Dimetrodon* (Fig. 43B,C) the origins of these muscles were probably displaced dorsally thereby bringing the line of traction more directly in line with the path of the point of insertion. The mechanical advantage gained by this arrangement is further developed in the cynodonts in which the supracoracoideus is positioned to rotate its point of insertion almost directly dorsally (Fig. 43D).

The history of the coracoid head of the triceps relates to its function as an extensor of the antebrachium and in more advanced forms as a retractor of the humerus. In *Diadectes* (and presumably in *Eryops*; Fig. 19A,B), it took origin immediately posterior to the glenoid and probably functioned only as an antebrachial extensor (Romer, 1922b: 537). In *Dimetrodon* (Fig. 19C) its origin is displaced sufficiently posterior to the glenoid that the olecranon would not only be pulled medially, hence antebrachial extension, but also posteriorly, thus effecting humeral retraction. In cynodonts this condition is accentuated, imparting a true posterior component to its traction. This condition is necessitated by the shift in glenoid orientation to a more posterior-facing position which would mask the origin of the coracoid triceps if it were not also displaced posteriorly. A coracoid head of the triceps is lacking in monotremes (McKay, 1894) as it is in other mammals. Superficially, at least, the posteriorly reflected coracoid process of monotremes is similar to that of cynodonts (Fig. 19F,G). In monotremes the coracobrachialis and a biceps head take origin from its apex (Westling,

1889 and Howell, 1937a) whereas in cynodonts it is here claimed that the coracoid head of the triceps arose from the apparently analogous position. However, a strong possibility exists that the monotreme pattern is indeed a primitive mammalian arrangement, and that the so-called coracoid process for the triceps in cynodonts bore the coracobrachialis and the short head of the biceps. In this case the coracoid triceps head would already have been lost. This problem cannot be solved without additional material demonstrating a more complete range of intermediate stages. At present there are so many known specializations in monotreme myology that no aspect of their locomotory anatomy can be assumed to be primitive prima facie.

The relative increase in size of the interclavicle undoubtedly correlates with the functional importance of the M. pectoralis. In *Eryops* (Fig. 19A) the interclavicle is a small plate anteroventral to the glenoid. It seems unlikely that pectoral musculature from such an origin alone could have effected the strong humeral adduction which is necessary in part to raise the body off the ground. Romer (1922b: 528) suggested that primitively the pectoralis took origin also from the sternum and surface of the M. rectus. In *Diadectes* and *Dimetrodon* as well as in *Sphenodon* and *Iguana* (Fig. 19B–E) pectoral musculature has extensive origin from an elongate interclavicle, evidence of powerful adduction and an increased ability to sustain the body above the ground. In cynodonts the interclavicle was proportionately as long as that in pelycosaurs and relatively wider. The deltopectoral crest (on which the M. pectoralis inserts) increased in relative length; in a typical specimen of *Dimetrodon* (MCZ 3357) the length of the crest is 36 percent of humeral length while in cynodonts it is commonly 50 to 55 percent or more. Some rather specialized cynodonts possessed a deep, ventral keel on the interclavicle that would appear to be direct evidence of a well-developed pectoralis. In African cynodonts an interclavicular keel was not an osseous structure but may have been present in cartilage. I conclude that cynodonts had increased power of humeral adduction and that the posterior extension of the interclavicle permitted more effective humeral retraction during the propulsive stroke.

The phylogenetic displacement of shoulder musculature leading to the cynodont arrangement increased the efficiency and power of locomotory movements already developed among earlier tetrapods: humeral rotation (subcoracoideus, scapulohumeralis anterior and subcoracoscapularis), humeral retraction (pectoralis, coracoid triceps), and humeral adduction (pectoralis). These changes are largely an improvement of a primitive system rather than innovation. Yet the position of the humerus and the orientation of the glenoid are substantially advanced toward a mammalian condition. It cannot be maintained that the cynodont shoulder girdle and forelimb were "primitive" or "reptilian"—any more than it can be maintained that they achieved a typically mammalian grade of organization.

PART THREE. APPENDICULAR SKELETON: PELVIS AND HINDLIMB

1. PELVIS (Figs. 44-47)

MATERIAL. The pelvis of *Cynognathus crateronotus* (BMNH R.2571; see Seeley, 1895b: 112-119) is one of the most complete cynodont pelves known to date. The iliac blade is missing from the left side and is only partially preserved on the right. Plaster has been utilized to rejoin the separate pieces particularly around the acetabulum and therefore the specimen is of little use in determining the nature of the hip joint. Otherwise this pelvis displays many features not preserved in any other specimen, notably the ventral junction between the two ischia and pubes.

The pelvis in *Thrinaxodon* is known adequately from a large number of specimens. The most useful is AMMM 5265 which preserves both ilia and the sacroiliac synchondrosis although the pubes and ischia are disarticulated and damaged. Numerous other specimens (AMNH 2228, BPI 287, NMB C.143, NMB C.318, NMB C.392 and SAM K.1395) provide additional material in various states of preservation and preparation.

An excellently-preserved right half of a pelvis is known in a Middle Triassic cynodont (BMNH TR.8) from the Manda Formation of Tanzania. The cranial fragments associated with this material are generically indeterminate, but may represent either *Scalenodon* or *Aleodon* (A. W. Crompton, pers. comm.). This cynodont possessed lumbar ribs of the *Cynognathus-Diademodon* type. The specimen is particularly important because the acetabulum is well preserved and is associated with a complete femur. Also from the Manda is a disassociated pubis of a generically indeterminate cynodont about twice the size of BMNH TR.8 (von Huene, 1950).

Broom (1905a: 99–100) described the ilium, ischium and pubis of *Diademodon mastacus*, but the specimen is not housed in any museum and is apparently lost. His incomplete account agrees in most details with the pelvic elements of *Diademodon* and *Cynognathus* described here from other sources.

Disarticulated ilia and ischia of *Cynognathus* and *Diademodon* are preserved in one collection (NMB C.2099; NMB C.2702), but generic separation of the individual bones is not possible. Another similar collection (BPI 1675) provides fragmentary pubes as well as ilia and ischia of these genera.

Haughton (1924: 89) described an ischium (TM 83) associated with *Glochinodontoides gracilis*; comparison with *Thrinaxodon* shows no substantial difference other than a larger size.

In the D.M.S. Watson Collection, there are a number of cynodont pelvic fragments, most of them generically indeterminate but very similar to the *Cynognathus-Diademodon* pattern. The most complete is DMSW R.225, a right half of a pelvis lacking only part of the iliac blade. In this specimen the suture between ilium, ischium and pubis is fused, retaining the three bones in their correct relative positions. Brink's (1955) description of the pelvis in *Diademodon* is apparently based on material in the D.M.S. Watson collection.

Broom (1932b: 239) claimed that in *Galesaurus* "the ilium is somewhat similar to that in *Thrinaxodon*, but more rounded and considerably higher". Since Broom's specimen is neither figured nor cited, the comparison is of doubtful significance—especially considering the inaccuracy of Broom's (1932b: fig. 91) figure of the ilium and pubis in *Thrinaxodon*. Parrington (1934) described the pelvis of *Galesaurus* from a specimen (UMC R.2722) which cannot be referred with certainty to this genus (see p. 62). Nevertheless, the specimen is undoubtedly galesaurid and morphologically is indistinguishable from *Thrinaxodon*.

A complete although disarticulated pelvis of *Leavachia duvenhagei* (RC 92; Broom, 1948: 626–627) is rather similar to other cynodont pelves except that the iliac blade has only a small posterior extension; this feature in contrast to other African cynodonts is similar to that developed in the South American traversodontid *Exaeretodon* (Bonaparte, 1963a; see discussion in Jenkins, 1970a).

Ilium

MORPHOLOGY. The cynodont ilium is composed of a thin, moderately expanded iliac blade separated from a base by a constricted neck (Fig. 44). The base bears a third of the acetabulum and facets for contact with the pubis and ischium. Anteriorly the blade outline in *Thrinaxodon*, *Cynognathus* and *Diademodon* is broadly rounded and somewhat spoon-shaped. Posteriorly the outline is angular with the straight posteroventral edge of the blade intersecting the gently convex dorsal (vertebral) edge at an angle of approximately 80°. The exact outline of the blade varies with ossification. In *Thrinaxodon* the dorsal edge often appears less convex than in larger cynodonts, imparting a lanceolate outline to the posterior terminus of the blade. The straight, evenly sloping dorsal edge of the *Diademodon* ilium figured by Broom (1905: Pl. I) undoubtedly represents an incomplete specimen. Brink (1955) also claimed that the upper (vertebral) margin of the ilium is perfectly straight; such a condition would approximate the morphology typical of primitive mammals. Brink's observation may have been based on DMSW R.225 in which the ilium appears to be straight. The iliac blade of this specimen is almost certainly incomplete and more complete specimens have an outline such as illustrated in Figure 44.

The anterior and dorsal edges of the iliac blade abruptly attenuate to a sharp rim; the rugosity of the rim is evidence of a cartilaginous supra-iliac blade. The deepest (highest) section of the blade often lies directly above the most anterior part of the acetabulum but marginal damage to all specimens leaves the true outline in doubt. The blade is uniformly rather thin except at the base, where the supra-acetabular buttress (*spa bu*, Fig. 44) contributes to the thickness, and along the straight posteroven-

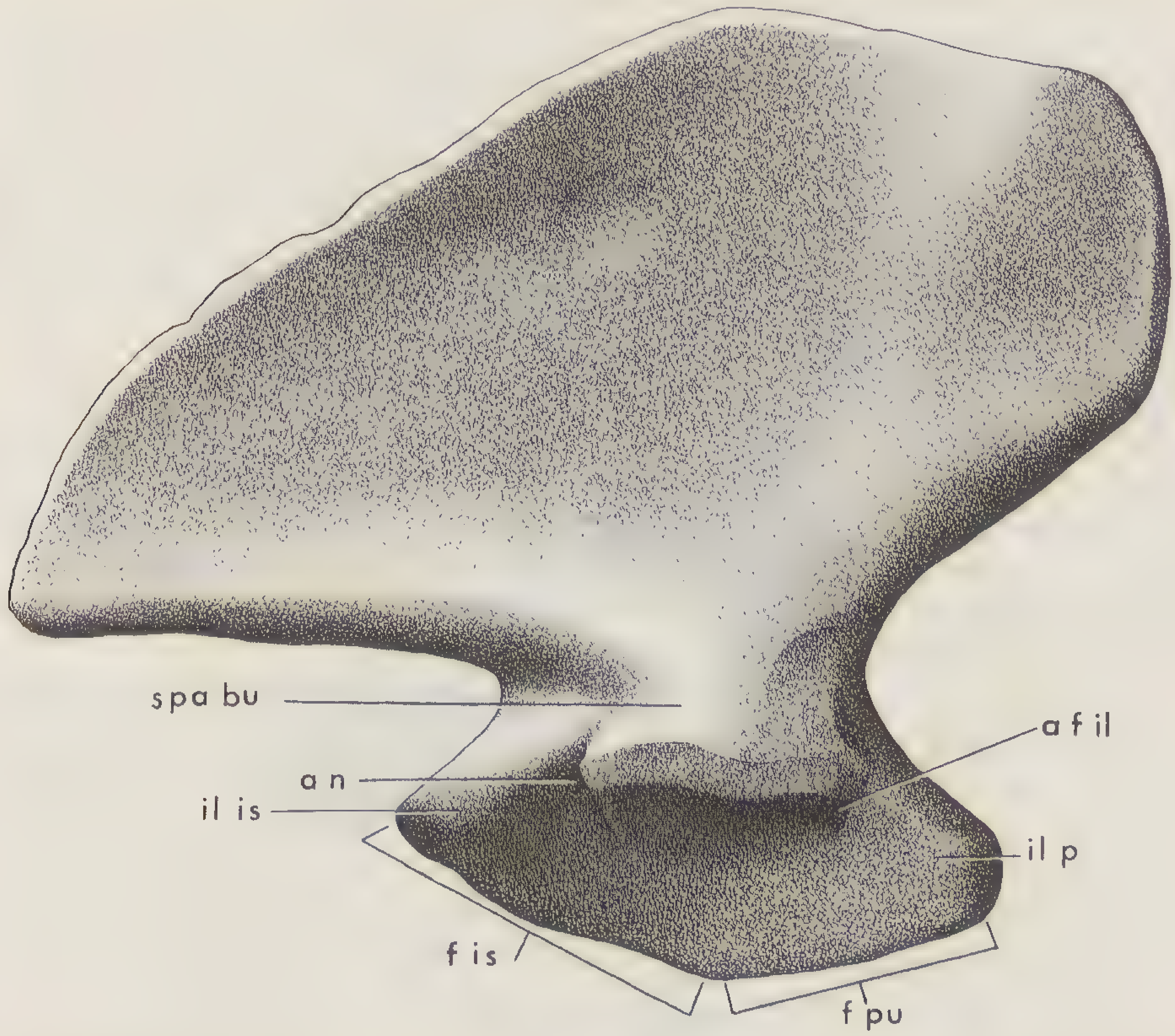

FIG. 44. Right ilium of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, in lateral view. The small, round depression in the center of the blade is probably the result of post-mortem damage, and perhaps represents a tooth mark. X1. Abbreviations: *a f il*, acetabular facet of the ilium; *a n*, acetabular notch; *f is*, facet for articulation with the ischium; *f pu*, facet for articulation with the pubis; *il is*, ischial process of the ilium; *il p*, pubic process of the ilium; *spa bu*, supra-acetabular buttress.

tral edge which is swollen into a rod-like buttress extending from the posterior end of the ilium to the supra-acetabular buttress. In *Diademodon, Cynognathus* and other cynodonts a slight thickening of the blade occurs in an area anterodorsal to the acetabulum. This thickening is manifested on the lateral surface of the iliac blade by a low, vertical ridge which thus delineates two shallow fossae of unequal size (Figs. 44, 46A); the anterior and smaller of the two fossae may represent some differentiation of the gluteal musculature, the mammalian homologue of the M. ilio-femoralis of reptiles. The bone surface texture of the entire lateral surface of the iliac blade is commonly smooth and devoid of muscle markings. In larger cynodonts the lateral surface may bear a small number of irregularly spaced striations radiating away from the neck (*st*, Fig. 45A). The medial surface of all cynodont ilia bears a pattern of striations radiating away from, but not quite reaching, the neck (*st*, Fig. 46B). Striations are most strongly developed on the anterior half of the blade where they may extend to the anterior and dorsal margin. The striations on the medial iliac surface record the presence of extensive connective tissue in the sacroiliac syndesmosis.

The base of the ilium is broad mediolaterally, consisting of a laterally projecting supra-acetabular buttress (*spa bu*, Fig. 44), an anteromedially directed process for articulation with the pubis (*il p*), and a posteromedially directed process for the ischium (*il is*). In many specimens the supra-acetabular buttress appears to be reflected somewhat dorsolaterally, and the pubic and ischial processes project ventrally and lie directly beneath the blade. This condition is unquestionably due to postmortem compression, for in the few relatively undistorted ilia (AMMM 5265, AMNH 2228, BMNH R.2571, NMB C.2699) the supra-acetabular buttress projects nearly as much laterally as do the pubic and ischial processes medially. The buttress is similarly developed in *Chiniquodon* (Romer, 1969a).

The iliac facet of the acetabulum is concave and faces for the most part directly ventrally (*a f il*, Figs. 44, 46A). The lateral rim of the facet is round; medially the anterior and posterior rims may converge and intersect at an 80° angle. In most specimens, however, the ossification is not sufficiently complete to distinguish the medial half of the facet from the lateral surfaces of the pubic and ischial processes and the facet appears to merge with these surfaces (Figs. 44, 46A).

Posterior to the supra-acetabular buttress is a deep recess, or so-called supra-acetabular notch (*a n*, Figs. 44, 46A, 50B). Broili (1908: 3–4) first called attention to this feature in dicynodonts, and noted its presence in *Cynognathus*. Romer (1922b: 581) concurred with Broili that it marked the position "of a ligament similar to that found in the cotyloid notch of the ischium of mammals". In mammals the homologous notch has shifted ventrally and, as Romer noted, the change in femoral position accounts for this displacement (*a n*, Fig. 50C). Two ligaments are associated with this notch in mammals: the transverse acetabular ligament and the ligament of the head of the femur (ligamentum capitis femoris). There is no direct evidence that cynodonts possessed a femoral head ligament. However, the acetabular notch of cynodonts was probably covered by a transverse acetabular ligament, thus creating a passageway for neurovascular structures supplying the femoral head and joint capsule.

The thickness of the pubic and ischial processes is approximately twice that of the iliac blade although the thickness is somewhat less along their juncture. The articular surfaces are strap-shaped, widening at the anterior (pubic) and posterior (ischial) ends (*f pu*, *f is*, Fig. 44). The pubic surface in well-preserved specimens is about three-quarters of the length of the ischial and faces more or less ventrally. The ischial surface faces posteroventrally and adjoins the pubic at an angle of from 130 to 150°.

Pubis

MORPHOLOGY. The pubis consists of a dorsal head, bearing the acetabular facet and articular surfaces for pubis and ilium, and a ventromedially directed blade. The acetabular facet, which faces posterodorsally as well as laterally, may be oval (*a f pu*, Fig. 45A) or may represent only part of an oval (*a f pu*, Fig. 46A); in either case its long axis is oriented posteroventrally. During life the cartilaginous articular surface was probably concave. In area the pubic facet is the smallest of the three facets comprising the acetabulum. Moreover the lateral rim of the pubic facet does not

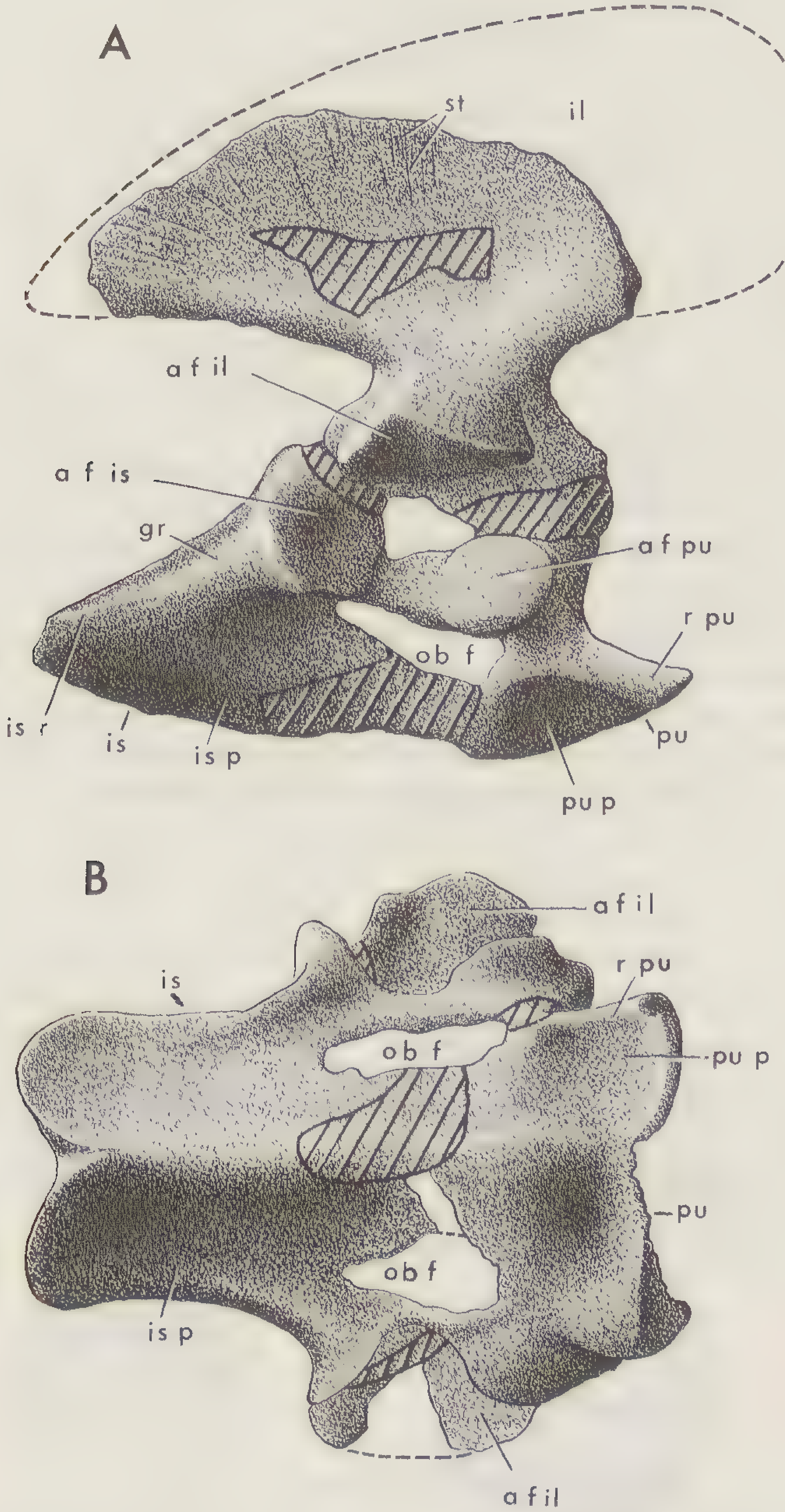

FIG. 45. Pelvis of the type of *Cynognathus crateronotus*, BMNH R. 2571, in A, lateral; B, ventral views. Oblique hatching indicates plaster reconstruction. Matrix adheres to the anterior part of the left pubis in B and it therefore appears to be different from right pubis. X0.45. Abbreviations: *a f il*, acetabular facet of the ilium; *a f is*, acetabular facet of the ischium; *a f pu*, acetabular facet of the pubis; *gr*, groove in dorsal edge of ischium; *il*, ilium; *is*, *ischium*; *is p*, ischial plate; *is r*, ischial ridge; *ob f*, obturator foramen; *pu*, pubis; *pu p*, pubic plate; *r pu*, rod-like anterodorsal edge of pubis, *st*, iliac striations.

protrude as far laterally as the iliac and ischial facets (Fig. 46A and DMSW R.225). This feature which opens the acetabulum more anteriorly than posteriorly is important in the determination of femoral position (see below).

The dorsomedial rim of the head of the pubis is occupied by a rugose, strap-shaped surface which articulates with the pubic process of the ilium. At its posterior terminus the surface faces posteriorly and makes contact with the ischium above the obturator foramen. The anterior half of the strap-shaped surface gradually expands to a wide terminus which together with the expanded anterior edge of the pubic process of the ilium represents the strongest part of the iliopubic symphysis.

Below the head the pubis is constricted to form a short neck. From the neck arises a ventromedially directed pubic plate which is laterally concave (*pu p*, Fig. 45A). Most of the pubic plate is thin and in no specimen is it completely preserved. The plane of the pubic plate appears to be slightly convolute because its anterior edge arises from the anteromedial surface of the neck whereas the posterior edge arises from the posteromedial surface. The anterodorsal edge of the pubic plate is swollen and rod-like (*r pu*, Figs. 45A, 46A), a primitive feature found is sphenacodontid and other pelycosaurs. The rod is slightly curved, bending ventrolaterally toward its anterior end. It terminates in a round, flat rugosity which has generally been interpreted (see below) as an articular facet for a prepubic bone. Opposing pubic plates meet along a thin symphysis, creating a broad, U-shaped basin which is deepest posteriorly along the puboischial contact. In no pubis is the anterior free edge completely preserved; presumably it was very thin and perhaps extended by cartilage. The posterior half of

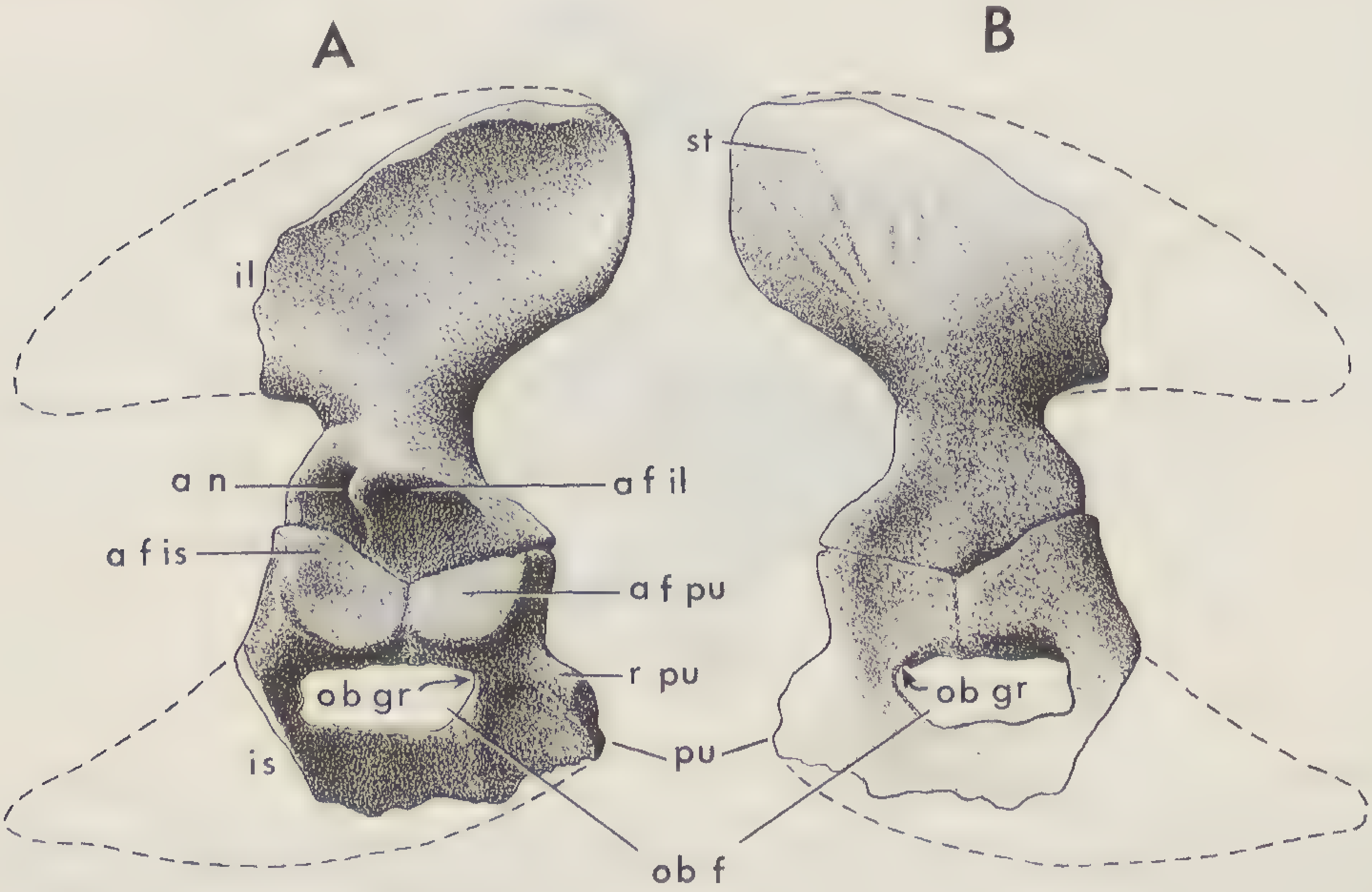

FIG. 46. Right side of the pelvis in a cynodont, BMNH TR.8, possibly referable to ?*Aleodon* or ?*Scalenodon*, in A, lateral; B, medial views. X1. Abbreviations as in FIG. 45 except: *a n*, acetabular notch; *ob gr*, groove across anterior edge of obturator foramen for the obturator nerve and vessels.

the pubic blade contacts the ilium beneath the obturator foramen. Spatulate in outline, this part of the blade is flat and of uniform thickness except along the obturator rim where it is slightly thickened.

Across the posterior edge of the neck of the pubis, which forms the anterior margin of the obturator foramen, runs a groove representing the course of the obturator nerve and vessels (*ob gr*, Fig. 46). The groove passes from the dorsomedial side of the neck to the ventrolateral side. This arrangement is essentially the same as in mammals.

The possibility of cynodont prepubic ("epipubic") bones has been suggested by many authors. Nineteenth century paleontologists (e.g., Owen, Seeley, etc.) often directly compared homologous bones in therapsids and marsupials and it is not surprising that the possibility of a prepubic ossification was introduced. Seeley (1895a: 40; 1895b: 116) stated that there is no evidence for an ossified prepubis in either *Microgomphodon* (=*Diademodon*) or *Cynognathus*. Nevertheless, later authors either restored a prepubis in cynodonts without eliciting evidence (e.g., Gregory and Camp, 1918: Pl. XLIV; Goodrich, 1930: 200; Howell, 1944: fig. 21) or claimed that a cartilaginous or osseous prepubis is rendered probable by the flat rugosity (?"articular facet") at the terminus of the rod-like anterodorsal edge of the pubis (Romer, 1922b: 580; Gregory, 1947: 37). No cynodont prepubes have yet been discovered, and it seems unlikely, in view of Vaughn's (1956) work, that separate prepubic ossifications were present. Vaughn adduced evidence to show that the prepubic bones of monotremes and marsupials "represent a retention or replacement of a portion of the reptilian puboischiadic plate anterior to the lateral pubic tubercle [and] that this retention or replacement took place during the general posteriorward displacement of the pubis . . ." (ibid.: 260). The cynodont pubis which lacks the pubic tubercle has undergone only a relatively small amount of posterior displacement; the anterior margin of the pubis projects craniad well beyond the acetabulum. The impetus for the formation of separate prepubic ossification was therefore lacking. It is probable, however, that the rod-like anterodorsal edge was continued in cartilage as was the analogous feature in many pelycosaurs (Romer and Price, 1940: 132). Further posterior displacement of the pubis may well have necessitated the strengthening of this cartilage through ossification but apparently the cynodont pelvis is functionally too reptilian to require this mammalian development. It is interesting to note that among tritylodonts, which are advanced therapsids with a very mammal-like pelvis, prepubic bones are known (Fourie, 1962).

Ischium

MORPHOLOGY. The ischium, like the pubis, is composed of a head and a ventromedially directed plate (*is p*, Fig. 47A,B). The head bears part of the acetabular surface for the femur as well as symphysial surfaces for the pubis and ilium. The acetabular facet of the ischium is approximately oval but its medial border (adjoining the ilium) is nearly straight (*a f is*, Fig. 46A). Ventrally the oval facet is narrower than dorsally and although poorly preserved in most specimens it was apparently concave during life. It faced anterolaterally and slightly dorsally (*a f is*, Fig. 46A; see also

DMSW R.225). The medial aspect of the ischial head bears a strap-shaped surface, which becomes broader dorsally, for articulation with the ischial process of the ilium (*f il*, Fig. 47B). This surface faces medially and dorsoanteriorly but at its cranial extremity it turns anteriorly to make a short contact with the pubis above the obturator foramen.

The neck between the ischial head and plate is short. A ridge extends from the middle of the lateral acetabular rim to the posterodorsal corner of the plate, gradually attenuating posteriorly (*is r*, Figs. 45A, 47A). At the posterodorsal corner it is terminated by a prominent but mediolaterally narrow ischial tuberosity (*is tb*, Fig. 47A–C). The extent of the ridge and the development of the tuberosity is variable. In *Glochinodontoides gracilis* (TM 83) the ridge does not extend to the ischial tuberosity but joins the dorsal edge of the ischial plate midway between head and tuberosity. In *Thrinaxodon* the ridge may fade into the lateral surface of the plate before reaching the ischial tuberosity, which is relatively small, or may be represented only as a lateral thickening of the dorsal rim. Between the ridge and the dorsal edge of the plate is a shallow groove which faces posterolaterally (*gr*, Figs. 45A, 47A). The groove is well developed in *Cynognathus*, *Diademodon* and *Glochinodontoides* but in *Thrinaxodon* it is variable—incipiently developed in some specimens (BPI 3848), apparently absent in others where the ridge is least pronounced (AMMM 5265).

The rest of the ischial plate below the ridge and tuberosity is thin and elongate anteroposteriorly, more or less rectangular and slightly concave medially (Fig. 47A,B). An entire ischial plate has not yet been recovered although that of *Cynognathus crateronotus* (BMNH R.2571) is nearly complete and the outline may be confidently reconstructed from this and other specimens (NMB C.2702, DMSW R.225). The posterior edge of the plate is straight, passing medially and ventrally to form a broad, V-shaped notch with the corresponding edge of the other ischium. The ischial symphysis is long and narrow with the articular contact somewhat thicker anteriorly than posteriorly. The ischial symphysis is approximately twice as long as the pubic. Broom's (1905a: 100) claim that the ischial symphysis in *Diademodon* is shorter than in *Cynognathus* was based on a specimen in which the posteromedial corner was apparently missing. No evidence of a difference in ischial morphology between these genera exists in the Bloemfontein collection (NMB C.2702). The anterior part of the plate is a very thin flange which meets the posterior edge of the pubic plate beneath the obturator foramen. Most specimens are incomplete in this region, the exceptions being that figured by Broom (1905a: fig. 4), DMSW R.225, and BMNH TR.8.

The relative size and configuration of the obturator foramen in cynodonts other than *Cynognathus* and an unidentified Manda cynodont (BMNH TR.8) must remain in doubt until more complete pelves are known. Broom (1932b: 271, fig. 91) described and figured *Thrinaxodon* as having no obturator but only a small pubic foramen. Later Broom (1948: 626–627) reiterated his belief by remarking that "in the only nearly perfect pelvis of *Thrinaxodon* which I have been able to examine, the pubes and ischia are imperfectly co-ossified, and in life probably a thin strip of cartilage separates the bones". The *Thrinaxodon* pelvis alluded to in Broom's (1932b, 1948) papers is, like so many of his other specimens, apparently lost. It appears that Broom's claim was based upon a poorly ossified or possibly damaged specimen. The pubes and ischia of known specimens of *Thrinaxodon* (AMMM 5265, BPI 3848),

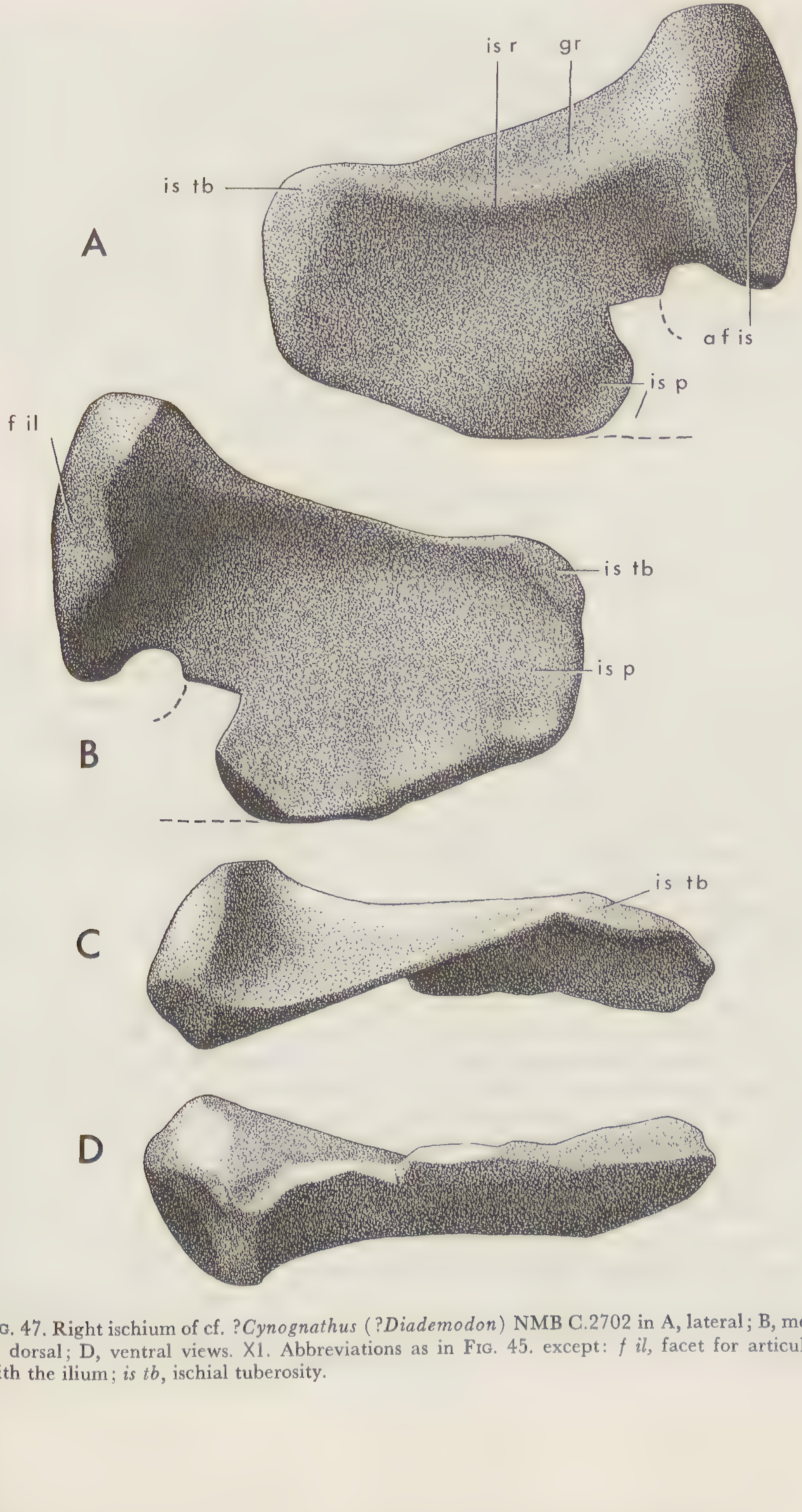

FIG. 47. Right ischium of cf. ?*Cynognathus* (?*Diademodon*) NMB C.2702 in A, lateral; B, medial; C, dorsal; D, ventral views. X1. Abbreviations as in FIG. 45. except: *f il*, facet for articulation with the ilium; *is tb*, ischial tuberosity.

although disarticulated, show clearly the characteristic indentations for the obturator rim, and therefore *Thrinaxodon* possesses an obturator foramen as do all other cynodonts for which the pelvis is known. In *C. crateronotus* (BMNH R.2571) the large, oblong foramen is two-thirds as long as the acetabulum (*ob f*, Fig. 45). In this specimen the anterior (pubic) rim appears to be somewhat more broadly rounded than the posterior (ischial) rim but in fact the anterior rim is not well preserved. Other pubes of *Cynognathus* or *Diademodon* (BPI 1675; both genera are most certainly represented in this collection but no differences in the pubes are apparent) show only the characteristic oblique cleft or obturator groove passing laterally and posteroventrally across the anterior part of the obturator rim. In the unidentified Manda cynodont (BMNH TR.8) the obturator foramen is more or less square with rounded corners and in this respect approximates the foramen shape typical of mammals. In Figure 46 the foramen appears to be rectangular; this is due to the two dimensional representation of the puboischiadic plate which is reflected medially.

2. HINDLIMB

Femur (Figs. 48, 49)

MATERIAL. Cynodont femora are adequately known in *Thrinaxodon* (SAM K. 1395; BPI 287, BPI 376; NMB 392) and in two collections in which disarticulated skeletons of *Cynognathus* and *Diademodon* are intermixed (BPI 1675, NMB C.2694). Except for differences of size and variations in ossification the femoral morphology is essentially the same for all three genera.

The proximal half of the femur associated with the type of *Cynognathus crateronotus* (BMNH R.2571) is poorly preserved. This fact accounts for various misconceptions, usually concerning the cynodont femoral head and trochanters, which are based on this one inadequate specimen.

The one known femur of *Glochinodontoides gracilis* (TM 83), described by Haughton (1924: 88–89), is only partially prepared but shows no significant differences from the above genera.

A large cynodont femur (SAM 977) in the South African Museum is identified as belonging to *Gomphognathus kannemeyeri*, one of the genera synonomized with *Diademodon* by Watson and Romer (1956: 65). In view of the lack of associated diagnostic cranial material (only a tibia is preserved with this specimen) this specimen is generically indeterminate and could represent either *Cynognathus* or *Diademodon*.

A well-preserved femur (BMNH TR.8) from the Middle Triassic Manda Formation of Tanzania is a particularly important specimen because it is associated with a nearly complete pelvis. The material, found with lumbar ribs of a *Cynognathus-Diademodon* pattern, is generically indeterminate but many represent either *Aleodon* or *Scalenodon* (A. W. Crompton, pers. comm.).

Seeley (1895b: 146–147) described a femur which he referred to *Tribolodon frerensis*. Broom (1905a: 100–101) described a femur of *Diademodon mastacus*. Neither of these incomplete femora could be located for reexamination but from the available

descriptions it appears that they conform morphologically to the femora described below.

Crompton (1955b: 628, 652, fig. 4) briefly described and figured the femur of *Cricodon metabolus* (UMC Field Catalogue No. 74) and made reference to the femur of *Scalenodon angustifrons* (UMC Field Catalogue No. 120A), both from the Manda Formation of Tanzania. Neither of these femora show any major differences from the *Cynognathus-Diademodon* pattern. von Huene (1950) also described femora from the Manda but all were disassociated and hence generically indeterminate.

The femur originally described by Parrington (1934: 57) as belonging to *Galesaurus* (UMC R.2722) lacked associated diagnostic cranial material and therefore may belong either to *Galesaurus* or to *Thrinaxodon*; it shows no differences from femora of *Thrinaxodon*.

MORPHOLOGY. The cynodont femur bears a distinct shaft which is moderately expanded at each end. The bone is straight except proximally where the shaft turns dorsomedially.

The head of the femur in *Thrinaxodon* is unossified. The proximal end is a flat, strap-shaped margin which runs in a hemicircle from the base of the (unossified) head to the greater trochanter (*h*, Fig. 49A,C). The margin is slightly expanded at the greater trochanter and widely expanded at the base of the head. There is no evidence that indicates that the head and greater trochanter were morphologically different from the better-ossified head and greater trochanter of larger cynodonts and therefore apparent differences are probably only artifacts of ossification.

In *Cynognathus* and *Diademodon* the proximal terminus from head to greater trochanter bears a rough texture typical of a cartilaginous cap. The head (*h*, Fig. 48C) is bulbous and somewhat oval in outline; its surface is confluent posteriorly with the crest leading to the greater trochanter, thus imparting a hemicircular outline to the proximal end of the bone. The amount of variation in the angle of the head among cynodont genera as cited by Crompton (1955b: 628) is probably spurious. Crompton claimed that in *Galesaurus*, *Glochinodontoides* and *Cynognathus* the head is only slightly reflected from the main axis of the shaft; in *Cricodon* and *Belesodon* the angle is supposedly greater while in *Traversodon* the angle is reputed to be 80°. However, as noted above, the head in *Thrinaxodon* and other small genera is unossified and therefore its orientation relative to the shaft cannot be determined with certainty. As preserved, the proximal end is truncated more or less transversely. This feature gives the appearance of little or no angle to the head. The femoral head in *Cynognathus* is quite unlike that in smaller cynodonts because much of it is ossified. The type, BMNH R.2571, is rather damaged and hence superficially appears to have little angulation. The femora of *Cricodon* (Crompton, 1955b: fig. 4) and *Belesodon* (von Huene, 1935–42: Pl. 15) are typical of larger cynodonts. The supposed greater angulation of *Traversodon* is almost certainly the result of postmortem damage to the incompletely ossified head. Similar distortions are often found in the femora of *Cynognathus* and *Diademodon*. The angle of the cynodont femoral head will be discussed in more detail in the following section.

The greater trochanter (*gr tr*, Figs. 48A,B,D; 49A,B,D), reflected dorsally, is slightly thicker than the ridge connecting it with the femoral head. The trochanter

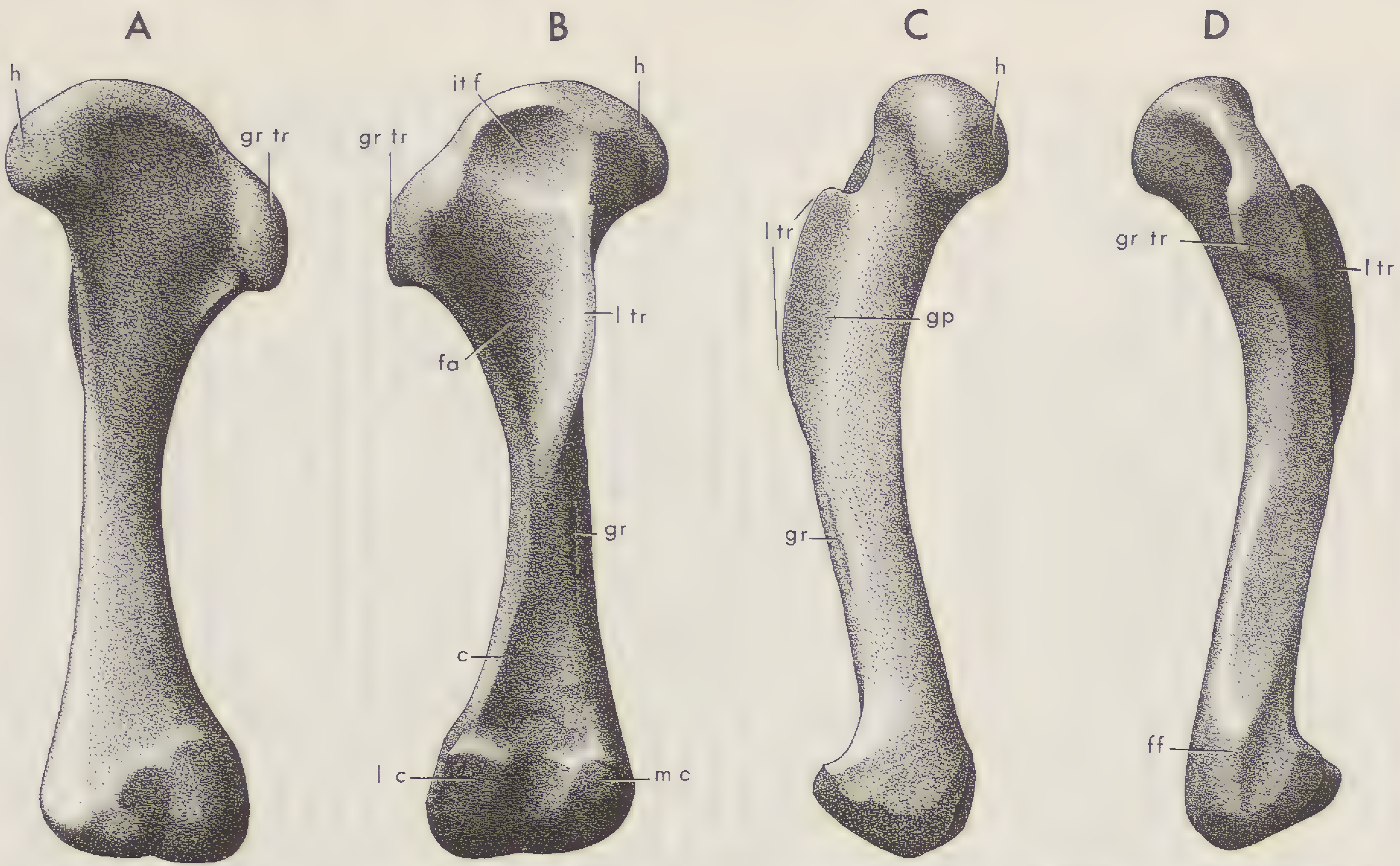

FIG. 48. Part I. Left femur of cf ?*Cynognathus* (?*Diademodon*) NMB C.2694 in A, dorsal; B, ventral; C, anteromedial; D, posterolateral views. X1. Abbreviations: *c*, crest between ventral and posterolateral surfaces of the femur; *fa*, fossa probably representing adductor musculature insertion; *ff*, point of femoro-fibular articulation; *gp*, groove between lesser trochanter and shaft, probably representing part of pubio-ischio-femoralis internus insertion; *gr*, groove of unknown function; *gr tr*, greater trochanter; *h*, femoral head; *it f*, intertrochanteric fossa; *l c*, lateral condyle; *l tr*, lesser trochanter; *m c*, medial condyle.

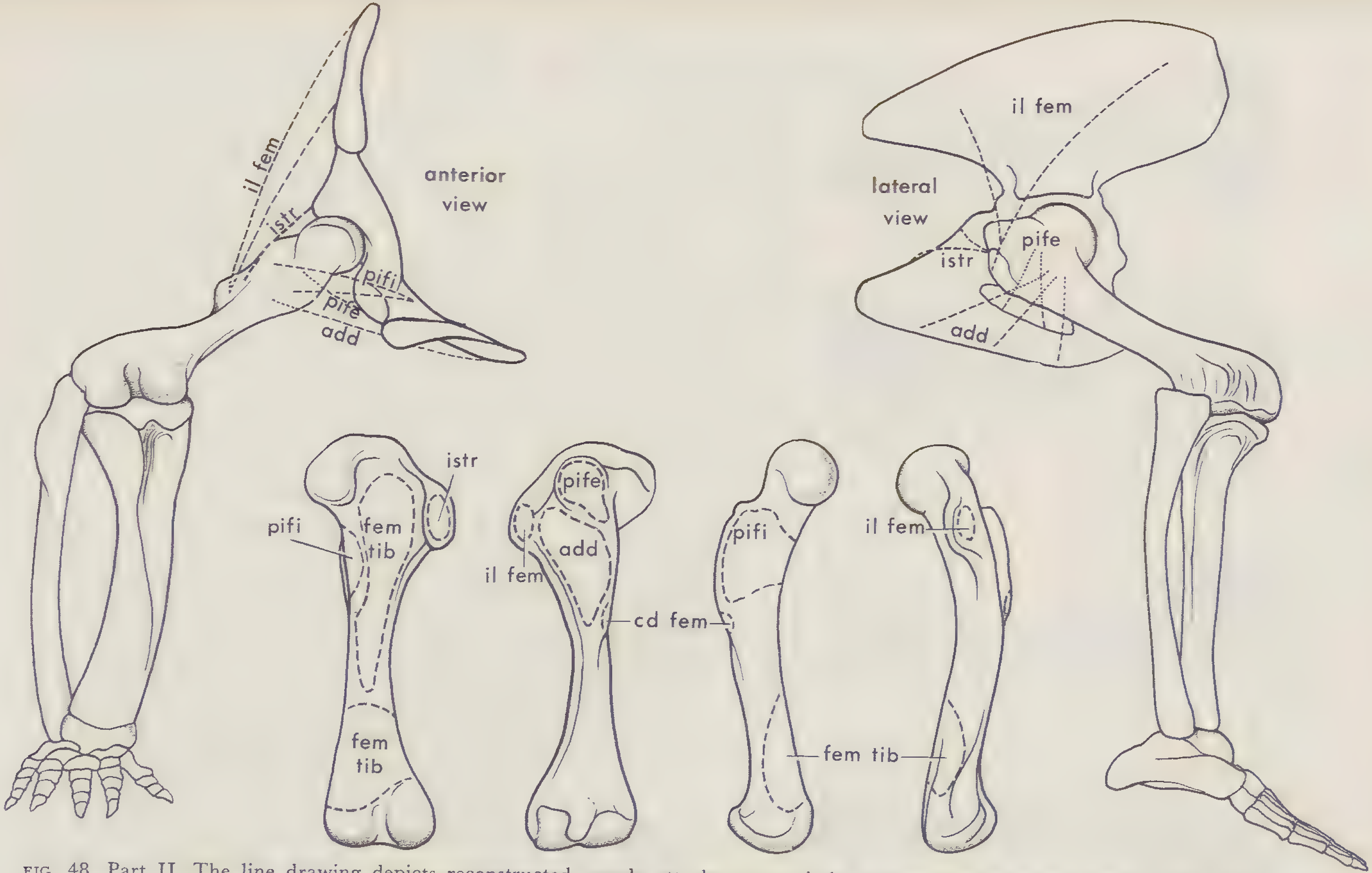

FIG. 48. Part II. The line drawing depicts reconstructed muscle attachments and the presumed orientation of some of the thigh muscles. Additional abbreviations: *add,* adductor musculature; *cd fem,* caudo-femoralis; *fem tib,* femoro-tibialis; *il fem,* ilio-femoralis; *istr,* ischio-trocantericus; *pife,* pubo-ischio-femoralis externus; *pifi,* pubo-ischio-femoralis internus.

bears two surfaces: one facing dorsoposteriorly, probably for the insertion of the M. ischio-trochantericus, the mammalian homologue of the Mm. obturator internus and gemelli; the other facing posteroventrally for the insertion of the M. ilio-femoralis, homologous with the mammalian gluteals.

The proximal dorsal surface of the femur (Fig. 48A) is recessed below the margin of the head and greater trochanter and gave origin to part of the M. femoro-tibialis, homologue of the Mm. vasti of mammals. The area of origin is smooth and shallowly concave. Traced distally the concavity gradually attenuates and terminates at the posterodorsal aspect of the shaft's midpoint. A similar origin for the vasti may be discerned in *Thrinaxodon* (Fig. 49A) but due to the incomplete ossification of the greater trochanter the nature of the ilio-femoralis and ischio-trochantericus insertions cannot be determined.

All African cynodont femora have a round, deep intertrochanteric fossa on the ventral surface between the humeral head and the greater trochanter (*it f*, Figs. 48B, 49B). This fossa undoubtedly represents the insertion of the M. pubo-ischio-femoralis externus, believed by Romer (1922b: 571–572) to be homologous with the obturator externus and quadratus femoris. Later Romer (1924: 102) rescinded this opinion, expressing doubt that the intertrochanteric fossae of therapsids and mammals were homologous. The solution to the question ultimately depends on the question of homology of the lesser and internal trochanters (to be discussed in a later section). Romer (1922b: Pl. XLVI) incorrectly located the insertion of the pubo-ischio-femoralis externus in *Cynognathus* as lying between the greater and lesser trochanters; such a condition would be analogous to that in pelycosaurs but in cynodonts the fossa is relatively smaller and more proximally located. Romer's misinterpretation of the fossa position in *Cynognathus* was apparently due to the poor preservation of the type specimen. Romer was probably correct, however, in believing that the pubo-ischio-femoralis externus insertion extended onto the lesser trochanter. The fossa is clearly seen to extend up to the proximal end of the trochanteric crest but there is no evidence that the insertion extended distally along the crest.

The lesser trochanter is a prominent flange which arises abruptly near the head and runs distally along the anteroventral aspect of the shaft (*l tr*, Figs. 48C, 49C). The flange is highest at the middle where it is reflected slightly anteriorly (Fig. 48B). Descending gradually the trochanteric crest terminates at about the shaft midpoint. In galesaurids the crest is continued to the medial epicondyle as a sharp edge between the ventral and anterior surface of the shaft (Fig. 49B). A similar feature was noted by Haughton (1924: 89) in *Glochinodontoides* and by Broom (1932b: 279) in *Galesaurus.* In *Cynognathus* and *Diademodon* the anterior and ventral surfaces distal to the lesser trochanter are confluent, the boundary between them marked only by a short, narrow groove (*gr*, Fig. 48B,C). The relative height and length of the lesser trochanter is much greater than in pelycosaurs or in mammals and this raises questions as to the disposition of associated musculature. The anterior surface of the trochanter forms a shallow groove where it meets the femoral shaft (*gp*, Figs. 48C, 49C); this area probably afforded an insertion for the M. pubo-ischio-femoralis internus which, according to Romer (1922b: 565–566), is homologous with the mammalian iliacus, psoas and pectineus. The opposite (posterior) side of the trochanter is bounded by a broad fossa attenuating distally as the shaft narrows (*fa*, Figs. 48B, 49B). This fossa,

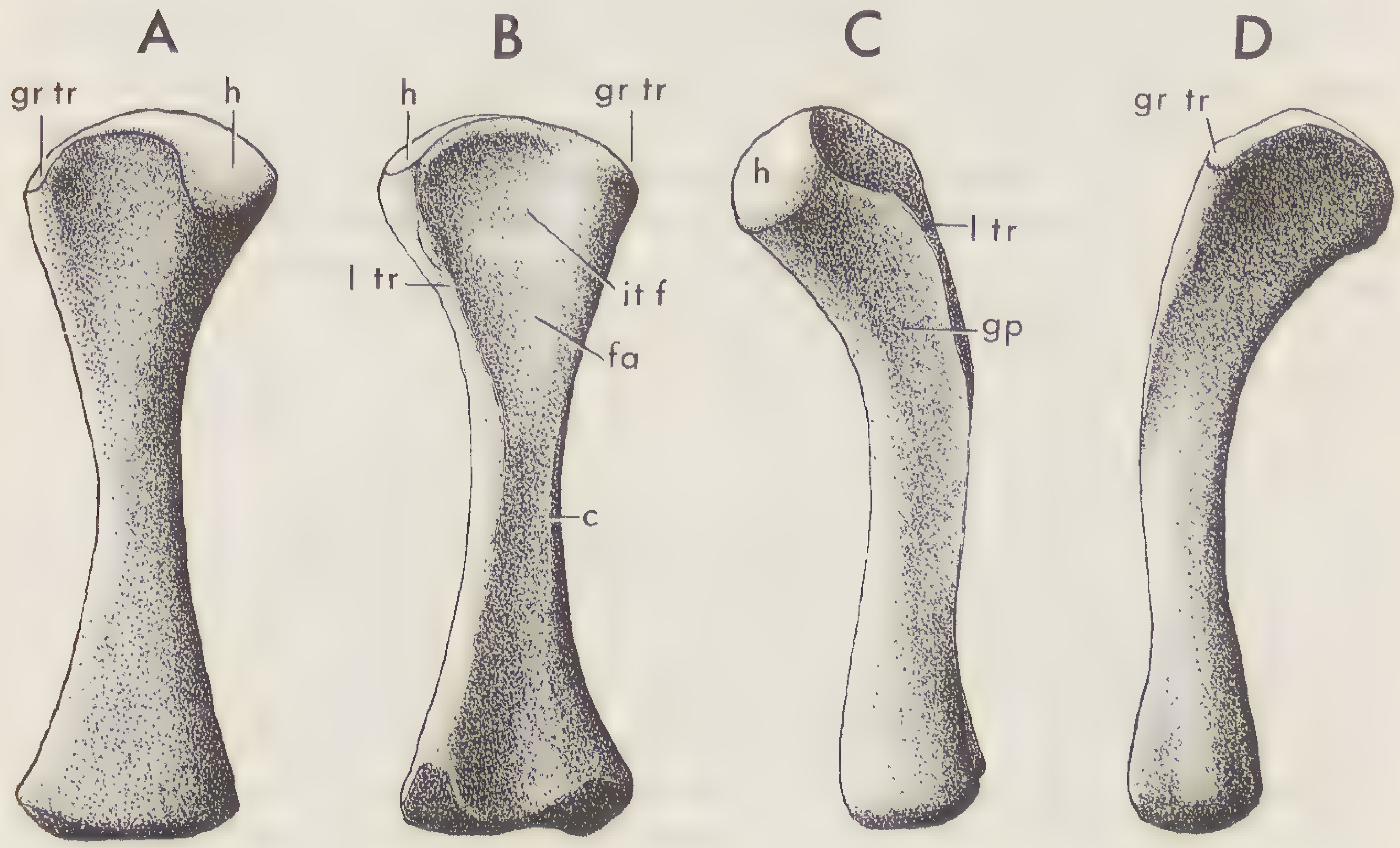

FIG. 49. Right femur of *Thrinaxodon*, SAM K. 1395, in A, dorsal; B, ventral; C, anteromedial; D, posterolateral views. X2. Abbreviations as in FIG. 48.

together with the posterior face of the trochanter, probably represents the insertion for the adductors which in living reptiles lies between the long flexors ventrally and the pubo-ischio-femoralis dorsally (Romer, 1922b: 571). The adductors probably did not extend distally beyond the midpoint of the shaft where the fossa terminates; in living reptiles the adductors are usually confined to the proximal half of the shaft whereas in mammals the insertion commonly extends distally almost to the origin of the gastrocnemius. Romer (1922b: Pl. XLVI) believed that the adductors in *Cynognathus* inserted in the shaft on the anterior side of the lesser trochanter. There are several reasons why such a reconstruction is less plausible than the one proposed above. First, Romer's figure of the ventral surface inaccurately portrays a ventrally facing surface anterior to the lesser trochanter onto which the adductors supposedly inserted. In fact the surface anterior to this trochanter faces anteriorly and provides no ventral surface for insertion. This area is occupied primarily by the M. pubo-ischio-femoralis internus as suggested above. Second, the adductor series inserts on the ventral aspect of the femur in recent lizards and mammals and the only analogous position in cynodonts is that suggested above. Moreover in *Dimetrodon* Romer and Price (1940: 149) recognized as well-developed adductor crest on the ventral surface of the femur between the fourth trochanter and the popliteal area. This contrasts to Romer's earlier, and I believe incorrect, interpretation (1922b: Pl. XLVI) in which the adductor insertion was reconstructed on the anteroventral aspect of the shaft adjacent to the fourth trochanter. From the adductor insertion in *Dimetrodon* as reconstructed by Romer and Price the adductor insertion of cynodonts and mammals can be derived without difficulty.

Romer (1922b: Pl. XLVI) showed that a fourth trochanter for the insertion of caudo-femoralis musculature is recognizable among most groups of Paleozoic tetrapods

and also is retained in the Dinocephalia (e.g., *Moschops*) as a tubercle at the distal end of the lesser trochanter. The lesser trochanter of cynodonts occupies a relatively much greater length of the femoral shaft than it does in any pelycosaur or other Paleozoic tetrapod. The proportionate length in cynodonts is approximately equal to the combined lengths of the internal and fourth trochanters of those earlier tetrapods which possess both. Therefore it seems probable that cynodonts possessed caudo-femoral musculature inserting along the distal half of the crest. In one specimen in the BPI 1675 collection the distal extremity of the lesser trochanter bears an irregular conformation which might indicate an insertion of a separate muscle. Romer (1922b: 584 and Pl. XLVI) claimed that a coccygeo-femoralis insertion is not recognizable as such in *Cynognathus* and that in mammals the muscle is displaced onto the greater trochanter as the piriformis (see also Gregory and Camp, 1918: 497). There is no evidence of such a displacement in any known therapsid and it appears that the lesser trochanter of African cynodonts may represent a conjoined lesser and fourth trochanter. This view is further confirmed by the "trochanter minor" of *Exaeretodon* which displays two distinct tuberosities (Bonaparte, 1963a: 29). The proximal and lower of the two represents the lesser trochanter; the distal and higher tuberosity, homologous with the fourth trochanter, is located near the shaft midpoint but is connected with the lesser trochanter by a distinct crest. The very elongate lesser trochanter of *Chiniquodon* extends considerably distal to the middle of the shaft (Romer, 1969a: fig. 9); Romer interpreted this feature as an adductor ridge—a reasonable possibility.

In *Cynognathus* and *Diademodon* the posterior and ventral surfaces of the femoral shaft are separated along an angular intersection or crest which runs from the greater trochanter to the side of the lateral condyle (*c*, Fig. 48B). In galesaurids the same feature extends from the greater trochanter only to the middle of the shaft (*c*, Fig. 49B); distally the junction of ventral and posterior surfaces is more rounded and less angular. Broom (1932b: 279) described this feature in *Galesaurus*.

The femoral shaft of cynodonts is approximately square in cross-section through its center but distally it expands anteroposteriorly so that it is rectangular in cross-section. The expanded dorsal surface of the distal end as well as the adjoining anterior (medial) and posterior (lateral) aspects of the shaft probably gave origin to additional parts of the M. femoro-tibialis. The other part of this muscle, discussed above, took origin from the proximodorsal aspect of the femur. Romer (1922b: 564) showed that the femoro-tibialis was differentiated early in reptilian evolution and that its disposition in living reptiles and mammals (Mm. vasti) remains unchanged.

The distal end of the femur in larger cynodonts bears a robust lateral (posterior) condyle (*l c*, Fig. 48B) and a somewhat narrower medial (anterior) condyle (*m c*). The medial condyle projects further ventrally than does the lateral condyle. Both condyles articulate with the proximal end of the tibia and do not represent, as Crompton (1955b: fig. 4) indicated, separate tibial and fibular condyles. The distal terminal surface in galesaurids appears to have been extensively cartilaginous and is often preserved only as a broad convexity (Fig. 49B) which truncates the shaft perpendicularly. However, well ossified larger femora show that a large part of the distal articular surface for the tibia lies at 45° to the shaft axis (Fig. 48C; contrast to pelycosaurs in which the distal articular surface is more or less parallel to the shaft axis).

The fibular head probably articulated with the lateral epicondyle as in pelycosaurs but this joint cannot have transmitted much weight. In some femora a slightly rugose, raised area on the lateral epicondyle (*ff*, Fig. 48D) marks the site of the femoro-fibular articulation.

The femur of the South American traversodontid *Exaeretodon* (Bonaparte, 1963a) conforms with Karroo cynodont morphology except for the addition of a distinct ridge ventral and distal to the greater trochanter.

FEMORAL POSITION IN CYNODONTS

Gregory (1912), Gregory and Camp (1918), Romer (1922b) and Vialleton (1924) are to be credited for the concept of functional reorientation of the limbs during the reptile-mammal transition. Their work on the hindlimb presented broad morphological comparisons between diverse femora and attempted to reconstruct muscle attachments in selected fossil genera by determining muscle homologies in living reptiles and mammals. The general conclusion is that therapsid femora are functionally transitional between typical femora of the two classes and that "the changed position of the proximal segments is the key to the therapsid and mammalian type of locomotor apparatus" (Romer, 1922b: 600). These major conclusions have been incorporated into much of the paleontological literature but in fact were rather ambiguously stated and poorly documented. These authors openly admitted to the paucity and poor preservation of the cynodont material available. While the general thesis of a functional reorientation of the limbs is certainly valid, the mechanics of the transition are by no means clear. If such a transition took place among therapsids the cynodont femur, of which Gregory, Camp and Romer had only a proximal end, must be posturally as well as structurally intermediate between pelycosaurs and mammals. Accordingly in the following discussion the femoral orientation of pelycosaurs as well as cynodonts will be reviewed.

Ideally, reconstruction of limb posture requires an associated skeleton in which the articular facets are clearly preserved. Among cynodonts, complete or nearly complete skeletons are known only from the smaller forms (i.e., galesaurids) in which the cartilaginous ends of long bones are not preserved. Since articular surfaces are the most critical factor, disassociated but better ossified long bones of larger cynodonts offer the only possibility of postural reconstruction. The fact that the proportional ratios of hindlimb elements is not always exactly known does not detract from the basic conclusions drawn from the facet orientations. In the following discussion the stated orientation of articular facets is based on well preserved femora and tibiae in the Bernard Price (BPI 1675) and National Museum (NMB C.2694, NMB C.2696) collections. Femoral orientation with respect to the pelvis and acetabulum is interpreted from a generically indeterminate Middle Triassic cynodont (BMNH TR.8; ?*Aleodon* or ?*Scalenodon*).

The reconstruction of femoral posture rests on interpretation of three critical joints: acetabular, femoro-crural and cruro-pedal. In pelycosaurs the acetabulum is a shallow, laterally directed concavity (Fig. 50A); the femoral "head" is merely a broad

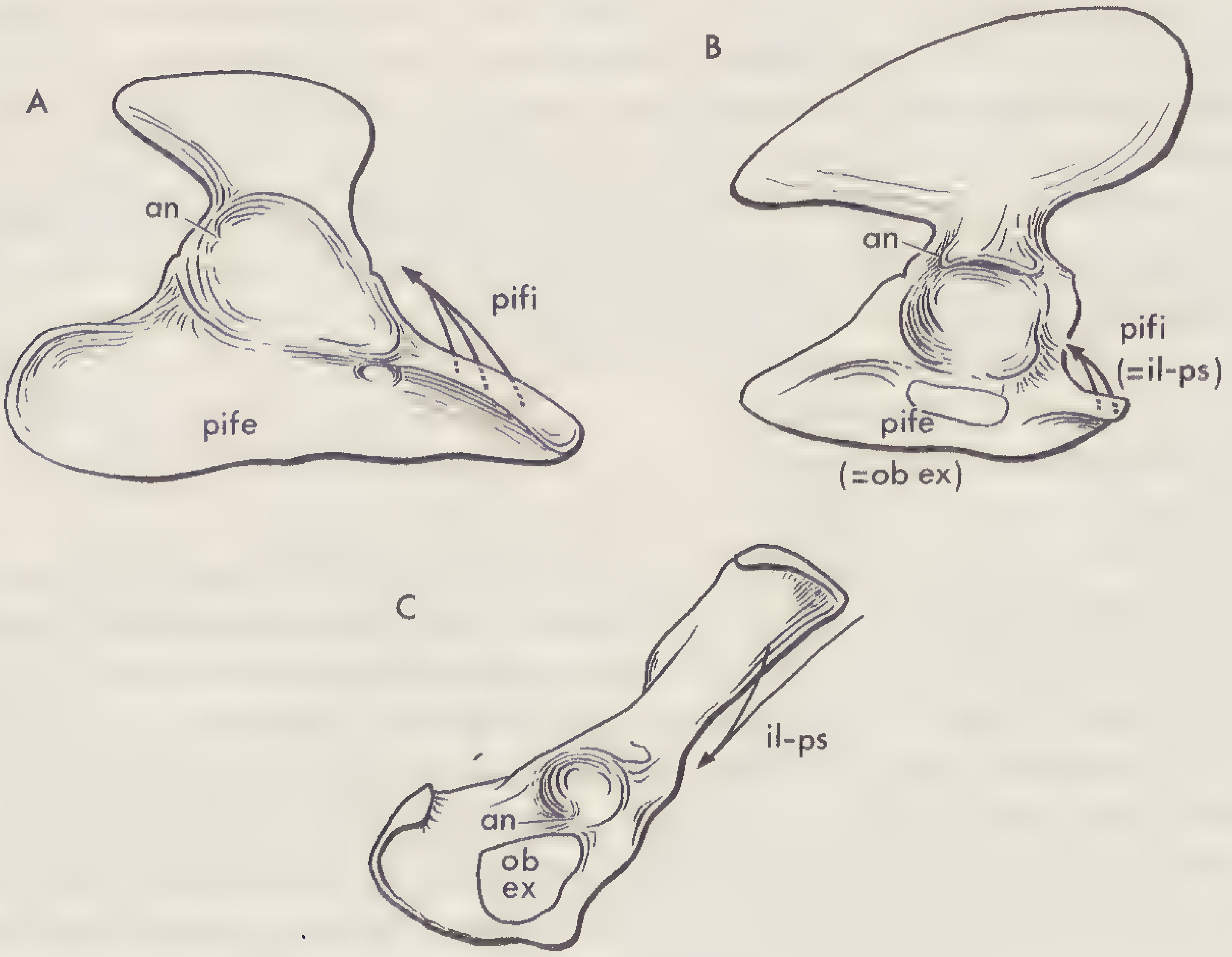

FIG. 50. Diagrammatic representation of the right half of pelves of A, a pelycosaur; B, *Cynognathus*; C, a mammal. *an*, acetabular notch; *il-ps*, ilio-psoas origin; *ob ex*, obturator externus origin; *pife*, pubo-ischio-femoralis externus origin; *pifi*, pubo-ischio-femoralis internus origin. Not to scale.

convexity on the distal end of the shaft (Fig. $54A_1$–A_3) but probably had a more rounded cartilaginous cap during life. There is no indication that the cartilaginous head was inflected medially or in any other direction. The articular surface as preserved truncates the shaft transversely to the shaft axis and probably indicates that the head was a bulbous, cartilaginous cap, the center of which lay on or near to the longitudinal axis of the femur. Therefore the femur must have projected laterally and nearly horizontally from the pelvis. Yet femoral position cannot be accurately determined from this articulation alone. The cruro-pedal articulation of pelycosaurs requires that the crus be directed ventrolaterally (Fig. 51A). The femoro-crural articulation is composed of the proximal tibial facets that are perpendicular to the long axis of the tibia and the femoral facets that are nearly parallel to the long axis of the femur, being directed primarily ventrally but also slightly laterally. This articulation also requires that the crus be directed ventrolaterally, but it requires a less oblique orientation (relative to the sagittal plane) than does cruro-pedal articulation. If the femur were held horizontally, the crus would be almost vertical, but then the distal end of the crus could not articulate with the pes. The solution to the apparent disparity in facet orientations requires that the distal end of the femur be slightly elevated above the proximal end (Figs. 51A; *dashed line*, 52B), a conclusion evidently reached by Romer (1922b: fig. 7).

Compared with the pelycosaurian pattern the hip, knee and ankle joints in cynodonts are substantially altered. At the knee joint the tibial facets transversely truncate

the proximal end of the tibia, as in pelycosaurs. However, the distal femoral facets for the tibia are no longer parallel to the femoral axis as in pelycosaurs but are inclined to an angle of about 45° to the femoral axis (see above, p. 172). This signifies that the distal end of the femur was held in a position lower than the level of the acetabulum (Figs. 51B, *heavy line*; 52B). Yet the cynodont condition is not more mammalian than

A

B

C

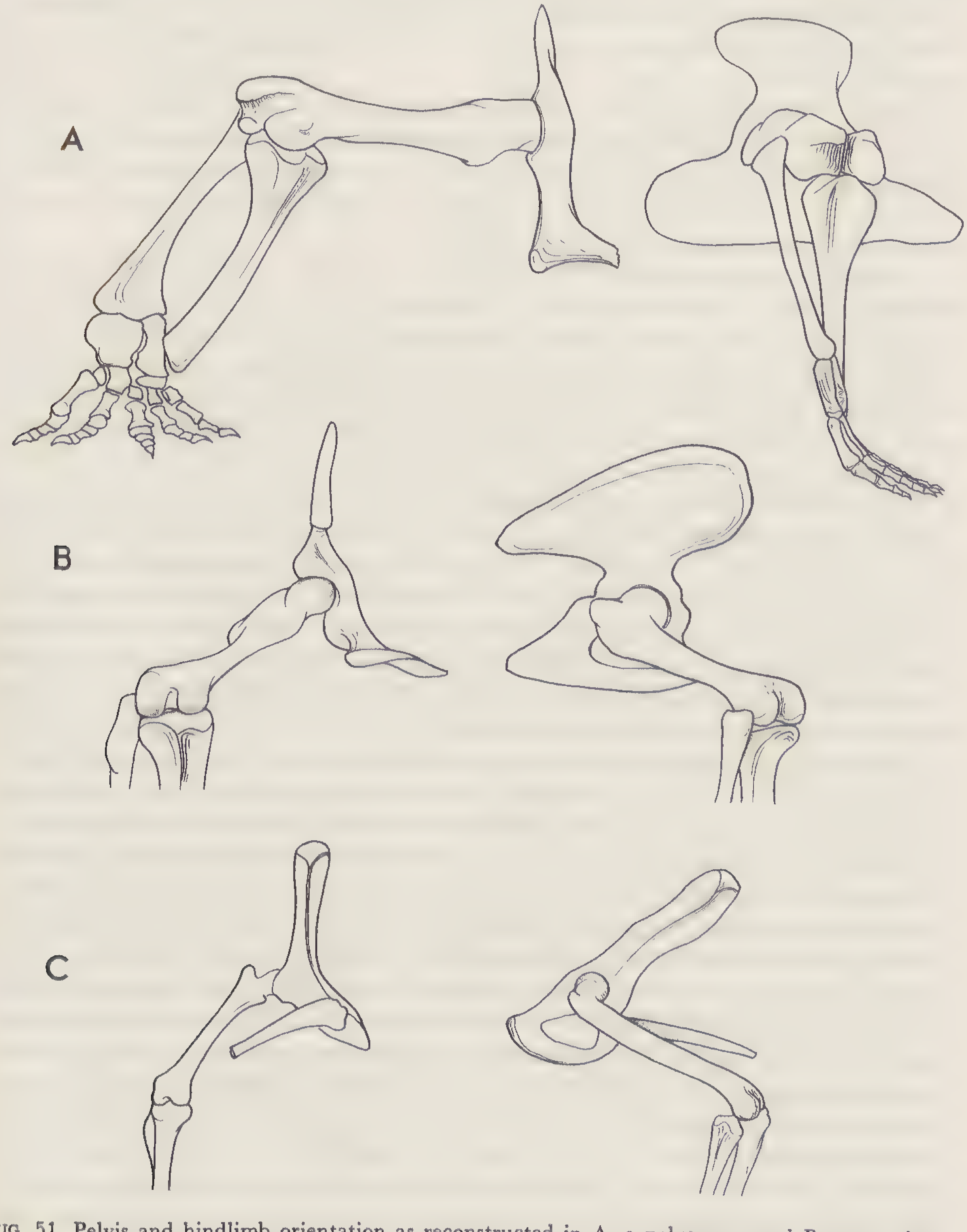

FIG. 51. Pelvis and hindlimb orientation as reconstructed in A, a pelycosaur and B, a cynodont compared with that in C, a mammal. On the left are anterior views, on the right lateral views. Not to scale.

the pelycosaur condition by virtue of the more distal (rather than ventral) orientation of the femoral facets. In most non-specialized mammals the distal articular facets represent a 90° arc from the ventral to the distal aspects of the femur. This wide arc permits a large amount of flexion and extension and is often further increased in cursorial specialization. In cynodonts the distal articular facets are intermediate—neither entirely distal nor ventral—but the orientation is a stage in the development of a mammalian type of facet for increased flexion and extension. The presence of cartilage on these facets in cynodonts could possibly have formed an arc essentially like that of mammals.

The major alteration in the cruro-pedal (ankle) joint of therapsids and of cynodonts in particular will be discussed in a following section. But to summarize, the evolution of a plantigrade pes was accompanied by a more vertical cruro-pedal relationship; this contrasts to the pelycosaurian condition in which the crus extended ventrolaterally to reach the tarsus (cf. Fig. 51A and B).

Neither the femoro-crural nor cruro-pedal articulations in cynodonts define precisely the posture of the femur, however. The morphology of the acetabulum and femoral heads are the determining factors in this regard. The pelvis of BMNH TR.8, although somewhat flattened (post-mortem) mediolaterally, demonstrates that the cynodont acetabulum had advanced toward the circular, deep socket form of mammals (Figs. 46A, 50). In life the iliac facet of the cynodont acetabulum probably projected farther laterally than either the pubic or ischial facets. This interpretation is based upon undistorted ilia (NMB C.2699) in which the pubic and ischial processes of the ilium are inflected medially. Consequently the rims of the pubic and ischial facets lay medial to the iliac facet (see Fig. 45B) and the acetabulum may be regarded as facing somewhat ventrally as well as laterally. Of course in mammals the acetabulum is also directed slightly ventrally concomitant to the more vertical orientation of the femur. The pelvis of BMNH TR.8 also shows that the pubic facet does not project as far laterally as the ischial facet. This feature is probably related to the anteriorly directed position of the cynodont femur.

The cynodont femoral head is not round and hemispherical as in mammals but is rather oval and bulbous (Figs. 48, $54B_3$). Furthermore the center of the head is not located on line with the axis of the shaft as it is in pelycosaurs but projects medially and dorsally. A quantitative estimate of the position of the femoral head of cynodonts relative to that in pelycosaurs and mammals now can be made with some degree of confidence. The orientation of a femoral head may be represented as a plane tangential to a point on its surface which is equidistant from the periphery. The orientation of the femoral head may then be expressed as an angle relative to the longitudinal axis of the femur. In cynodonts with well-ossified femoral extremities this angle appears to have been on the order of 55° compared with the 80° orientation in pelycosaurs or a typical mammalian angle of 25° (Fig. 52A). The "head" of the pelycosaurian femur is never more than a broad convexity on the proximal end; for reasons noted above the femur projected laterally and the head was undoubtedly a cartilaginous cap set perpendicularly to the shaft. The intermediate position of the cynodont femoral head is indicative of a shift toward a more mammalian femoral posture. Specifically, the angle between the long axis of femur and the parasagittal plane (*vertical line*, Fig. 52A) becomes more acute. In generalized, non-cursorial mammals the femur usually

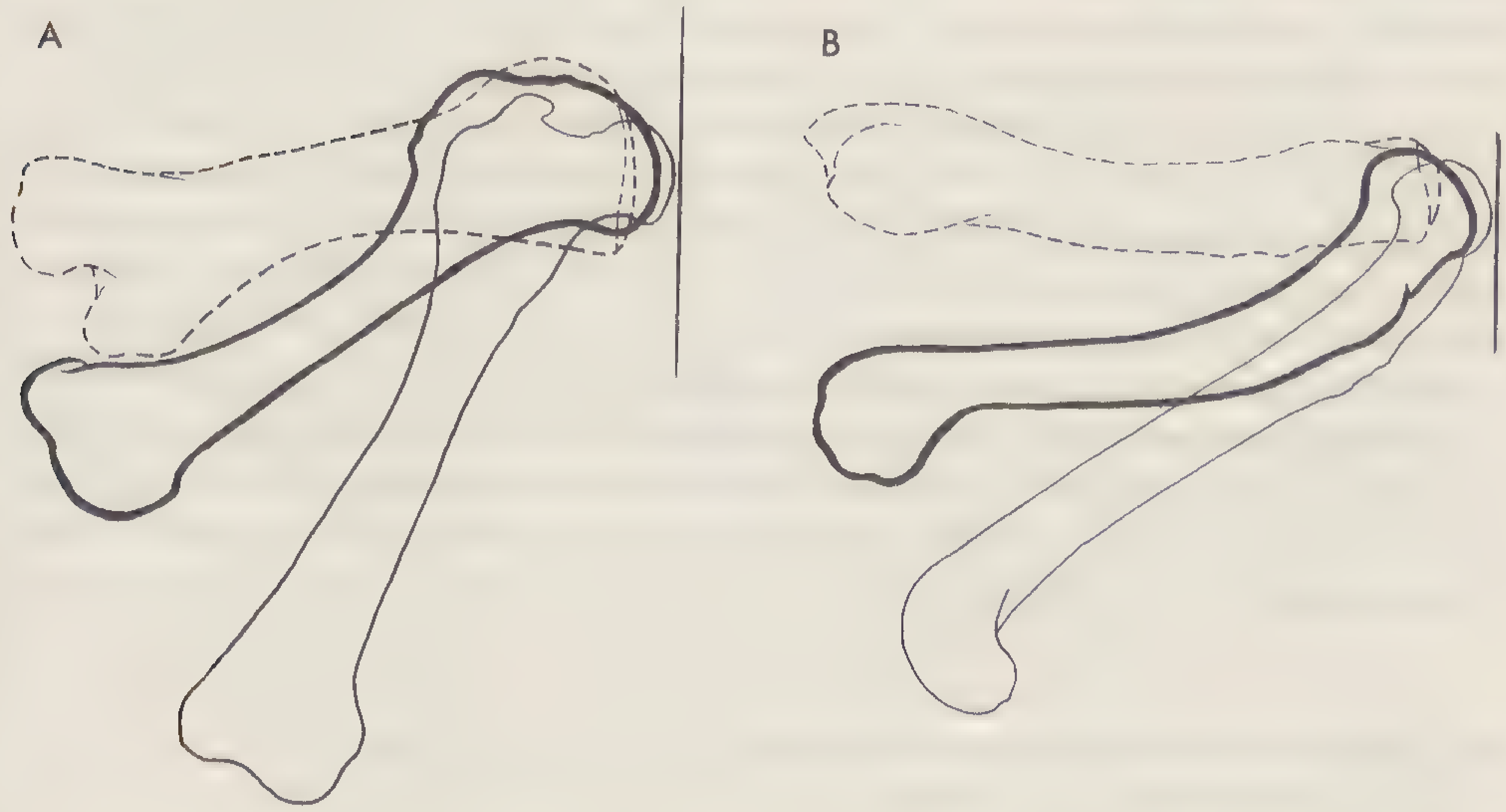

FIG. 52. A, dorsal views: B, anterior views of femoral posture in pelycosaurs (dotted line), cynodonts (heavy line), and generalized mammals (narrow line). The vertical line in both A and B represents a parasagittal plane through the deepest part of the acetabulum. Not to scale.

projects obliquely away from the body axis at angles of 20 to 25°. Thus the cynodont femur occupies a truly intermediate position between that of primitive synapsids and their mammalian descendants.

The cynodont femur, viewed from either medial or lateral aspect, shows that the proximal end and head are reflected dorsally relative to the rest of the shaft (Fig. 52B). This condition, apparently absent or little developed in pelycosaurs, is retained by generalized mammals although not in such extreme form (Fig. 52B). Thus the cynodont and mammalian femoral head is directed not only medially but also dorsally. The functional significance of this feature appears to be related to the evolution of a mammalian pattern of femoral posture and movement.

In pelycosaurs forward thrust was transmitted to the pelvis as the femur swung posteriorly in a horizontal arc. But even in its most posterior position the femoral axis probably did not form an angle smaller than 45° with the body axis because neither the head of the femur nor the acetabulum appear to have been sufficiently rounded to permit such a posture. At no point in the locomotory cycle was the femoral head directed more anteriorly than medially; thus transmission of forward thrust was mechanically inefficient and undoubtedly relied on strong ligamentous and perhaps muscular control of the forces generated. At any time during the propulsive stroke, medially directed components comprised a significant part of the total force generated.

Among therapsids the inefficiency of the pelycosaurian type of femoral head would have been rendered more acute by the tendency to shift the femur beneath the body, i.e., by displacing its distal end anteriorly and ventrally. In such a position a head situated on the proximal end and perpendicular to the shaft axis is poorly suited to transmit forward thrust. Therefore the cynodont femoral head develops medially to compensate for the anterior displacement of the distal end of the shaft. The dorsal reflec-

tion of the head, however, is a function of the ventral displacement of the distal end of the shaft. As the distal end of the femur swings ventrally and posteriorly during locomotion a forward and upward thrust is transmitted to the acetabulum. However, the cynodont femur is not aligned with the body axis at an angle of 25° or less, as in mammals, but instead lies at about 55°. This intermediate posture results in an arc of femoral movement which is neither nearly horizontal, as in pelycosaurs, nor nearly vertical, as in mammals. As a result the femur must bear propulsive forces on the dorsal aspect of its proximal end necessitating a somewhat dorsally directed femoral head.

In some generalized, non-cursorial mammals a slight dorsal reflection of the femoral head is retained. It is apparently correlated with a femoral posture in which there is a relatively large angle (approximately 25° or more) between the femoral and body axes. In other mammals whose femora are posturally less oblique to the body axis the dorsal reflection of the head is altogether lost.

THE HOMOLOGY AND FUNCTIONAL EVOLUTION OF THE MAMMALIAN LESSER TROCHANTER

Questions of homology between various trochanteric structures of the femur have always been of paleontological interest because trochanters mark the insertion of major pelvic muscles. Homologous trochanters imply homologous musculature although not necessarily similar functional patterns. The homology of trochanters in fossil forms is therefore a basic consideration in interpreting functional anatomy; if trochanters occur in an analogous position on femora of related species but are not considered to be homologous, the question is immediately raised as to why one replaced the other.

The homology of the internal trochanter (trochanter internus) of reptiles and the lesser trochanter (trochanter minor) of mammals has been both accepted and rejected primarily on the basis of fossil evidence. The lesser trochanter of mammals is principally the site of insertion of ilio-psoas musculature which is particularly important in protracting (or flexing) the femur. The lesser trochanter in typical position lies below the level of the acetabulum, and since it occurs on the medial aspect of the shaft, it is positioned nearly beneath the acetabulum as well. The internal trochanter of living reptiles is associated principally with the insertion of a major adductor muscle, the pubo-ischio-femoralis externus. With regard to its position relative to other femoral features, the internal trochanter is analogous to the lesser trochanter. It lies below the level of the acetabulum but because reptilian femora are oriented more horizontally than vertically the trochanter lies lateral to the acetabulum rather than directly beneath it. Nevertheless the internal trochanter lies on the anteroventral aspect of the reptilian femur which is the morphological equivalent of the medial aspect of the mammalian femur. In the following review of the evolution and homology of the mammalian lesser trochanter, the term "anteroventral trochanter" is applied to those trochanters of fossil forms which are in the position of an internal (reptilian) or a lesser (mammalian) trochanter but which cannot be positively designated as either.

Gregory (in Gregory and Camp, 1918: 534) accepted the homology between the reptilian internal and the mammalian lesser trochanter. He cited the fact that the trochanter in reptiles is associated with the insertion of the pubo-ischio-femoralis internus

and externus muscles, whereas in mammals the apparent homologue of the pubo-ischio-femoralis internus, the ilio-psoas, inserts on the lesser trochanter. The fact that the obturator externus, the mammalian homologue of the pubo-ischio-femoralis externus, did not insert on the trochanter (as in reptiles) was not discussed.

Romer (1922b: 566) concluded that the internal trochanter is only the "partial homologue" of the lesser trochanter because, as first shown by Gregory, the muscular insertions of homologous muscles were not exactly similar in relation to the trochanter. Later Romer (1924) entirely rejected the homology between the reptilian internal and the mammalian lesser trochanter. Romer's conclusion, based largely on fossil evidence, has never been challenged. Howell's (1941) detailed comparative study confirmed Romer's conclusions that the reptilian internal trochanter and the mammalian lesser trochanter are not homologous because they represent the attachments of non-homologous muscles. Howell emphasized that the internal trochanter of living reptiles such as *Iguana* is associated with muscles of tibial and obturator innervation, whereas the lesser trochanter of mammals represents the attachment of muscles of femoral innervation. Howell was careful to point out, however, that living reptiles are specialized myologically, and "have probably departed farther from basic reptiles in the plan of their hip musculature than have mammals". The point of interest therefore is no longer the question of homology between internal and lesser trochanters but the evolutionary development of the latter. Parrington (1961) adduced evidence to support the view that cynodonts had a mammalian lesser trochanter and that the supposed transition from a pelycosaurian internal trochanter occured during a pre-cynodont stage. Romer and Price (1940) had previously concluded that the pelycosaurian internal trochanter represents the attachment of the pubo-ischio-femoralis externus muscle, and thus is homologous with the internal trochanter of living reptiles. If both Romer and Price (1940) and Parrington (1961) are correct, then a major change in trochanter morphology occured between pelycosaurs and cynodonts with the lesser trochanter replacing the internal trochanter. Such a change might be expected to accompany the development of an essentially mammalian type of pelvis. However, the paleontological evidence, discussed below, does not support the view that the supposed origin of the mammalian lesser trochanter was accompanied by the evolution of a typically mammalian system of pelvic musculature. In order to present a comprehensive survey of this evidence, a summary and critique of both Romer's and Parrington's contributions must be given.

Romer (1924) established that the trochanteric structure of a primitive therapsid such as *Deuterosaurus* is basically similar to that of pelycosaurs. Basing a reconstruction of musculature on the condition in living reptiles, *Iguana* in particular, Romer concluded that in pelycosaurs and primitive therapsids the pubo-ischio-femoralis externus inserts into the intertrochanteric fossa and on the adjacent internal trochanter (*pife*, Fig. $54A_2$). The association of the trochanter and fossa with the same muscle insertion is particularly clear in some pelycosaur femora where a rugosity may be traced from the fossa to the trochanter. The muscle interpreted to have inserted here took origin from the lateral aspect of the pubo-ischiadic plate (*pife*, Fig. 50A). Romer further concluded that the pubo-ischio-femoralis internus in both therapsids and pelycosaurs inserted on the dorsoproximal and anteroproximal surface of the shaft; in pelycosaurs, at least, this area extends from near the ilio-femoralis insertion (the site of the

greater trochanter in mammals) anteriorly and then ventrally across the anterior face of the internal trochanter (*pifi*, Fig. $54A_1$). In cynodonts, however, the exact disposition of the insertion is rather conjectural. Romer claimed that a femur of *Diademodon* has a muscle scar on the anterodorsal aspect of the proximal end which delimits the border between the pubo-ischio-femoralis internus (or ilio-psoas) and the ilio-femoralis (gluteal) muscles, the latter inserting on the greater trochanter. According to this interpretation the pubo-ischio-femoralis internus inserted anterior to the greater trochanter, but Romer did not state whether he believed the insertion extended anteroventrally onto the face of the internal trochanter. Romer's ultimate contention was that this muscle scar represents the incipient lesser trochanter which subsequently migrated anteroventrally to take the place of the internal trochanter.

Parrington (1961: 295) reported that the supposed pubo-ischio-femoralis internus insertion of Romer could not be identified on any of the well-preserved cynodont femora available. Similarly, this feature was not present on any of the many cynodont femora examined during the course of this study. Nevertheless the absence of this feature does not obviate the possibility that the pubo-ischio-femoralis internus insertion in cynodonts was similar to that in pelycosaurs—which in essence is Romer's conclusion (*pifi*, Fig. $54B_1$).

The crux of Romer's argument is based on the apparent difficulty in explaining "the diverse tendencies [of trochanter location] seen in a morphological series of femora" (Fig. 53). Romer attempted to show that the internal trochanter of therapsids displaces posteriorly and diminishes in size during the pelycosaur-therapsid transition (Fig. 53A–C). Then the trochanter enlarges and displaces anteriorly (Fig. 53D) at the monotreme level of organization. Finally, the trochanter moves ventrally and anteriorly again among therian mammals (Fig. 53E,F). Since it is difficult to account for two reversals in the evolutionary continuum from pelycosaurs to mammals, Romer concluded that the internal trochanter moved posteriorly and finally was lost, only to be

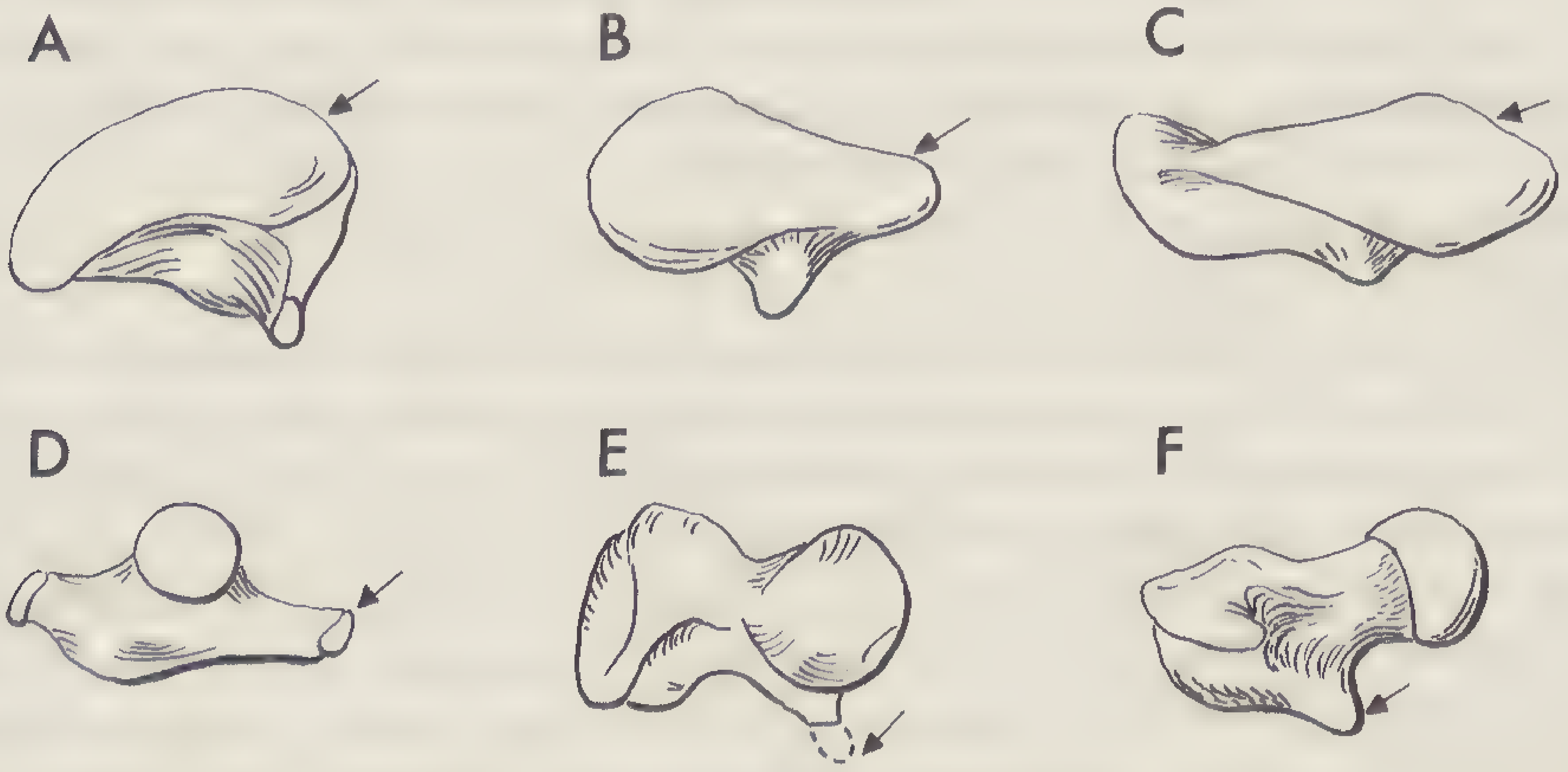

FIG. 53. The evolution of the trochanter minor of mammals as interpreted by Romer (1924). The arrow indicates the insertion of the ilio-psoas and homologues and, according to Romer, represents the mammalian trochanter minor or its homologue. After Romer, 1924: fig. 3. A, *Dimetrodon*; B, *Deuterosaurus*; C, *Cynognathus*; D, *Ornithorhynchus*; E, *Pachyaena*; F, modern placental. Not to scale.

replaced by a lesser trochanter which migrated ventrally from the dorsoproximal surface. Therefore the trochanters in question are not homologous between synapsids and mammals.

Romer's evidence for a de novo origin of the mammalian lesser trochanter is inconclusive because it fails to demonstrate that a vestigial internal trochanter and an incipient lesser trochanter coexisted in some transitional therapsid. Parrington (1961) attempted to provide just such a piece of evidence by a comparative study of therapsid femora. Parrington recognized that theriodont femora may be grouped into three taxonomic-morphologic categories: 1) titanosuchids and gorgonopsids; 2) therocephalians and primitive bauriamorphs; and 3) cynodonts and tritylodonts. The femora of the cynodont *Cricodon* and the tritylodonts *Bienotherium* and *Oligokyphus* make a convincing morphological series between the cynodont and the monotreme condition. On this account Parrington concluded that the cynodont trochanter is homologous with the mammalian lesser trochanter and that the internal trochanter to lesser trochanter transition occurred among more primitive therapsids. Since cynodonts are the only advanced therapsid group known from which, on evidence of cranial osteology and dentition, mammals could have been derived, Parrington's deduction is logical. However, if the cynodont trochanter on the anteroventral aspect of the shaft is the lesser trochanter then the expected arrangement of the pubo-ischio-femoralis internus muscle should be that of its mammalian homologue, the ilio-psoas group. To the contrary, the pelvic conformation of cynodonts suggests that a basically pelycosaurian pattern was retained. In pelycosaurs the pubo-ischio-femoralis internus probably arose from the medial aspect of the pubic plate just as in living reptiles where there is often a distinct shelf (Romer, 1922b: 565-566; *pifi*, Fig. 50A). An analogous shelf is present in cynodonts (Fig. 50B). In mammals the ilio-psoas group takes origin from the lumbar vertebrae and either an external, anteroventrally facing shelf on the ilium (*il-ps*, Fig. 50C) or the internal surface of the ilium. There is no indication of such a shelf on the flat, plate-like cynodont ilium, despite the claim by Parrington, who recognized this difficulty, that the height of the iliac blade "invites the interpretation that ventrally it accommodated the iliacus, or combined iliaco-psoas muscle, in the mammalian manner" (Parrington, 1961: 288). The internal surface of the ilium could not have been the site of origin for a mammalian iliacus because it was occupied by the extensive sacroiliac articulation. Contrary to Parrington, the shape of the cynodont ilium is here construed as evidence that the ilio-psoas muscles were not disposed in a mammalian fashion. This interpretation leads to an apparent paradox: cynodonts possessed a mammalian lesser trochanter but retained a basically reptilian origin for the muscles that are associated with this trochanter in mammals.

Parrington correctly regarded the anteroventral trochanter of titanosuchian and gorgonopsid femora as being homologous with the similarly located trochanter of pelycosaurs. The transition from an internal trochanter to a lesser trochanter according to Parrington's view is represented by the femora of a Late Permian whaitsid therocephalian and an Early Triassic scaloposaurid bauriamorph. Parrington's whaitsid femur (Fig. 54C) shows a posterodorsal proximal trochanter identified as the greater trochanter (*gr tr*, Fig. 54C) and a posteroventral trochanter immediately beneath it identified as the internal trochanter (*x*, Fig. $54C_2$,C_3). Near the proximal end of the shaft along its anterodorsal aspect is a ridge that Parrington regarded as marking the point

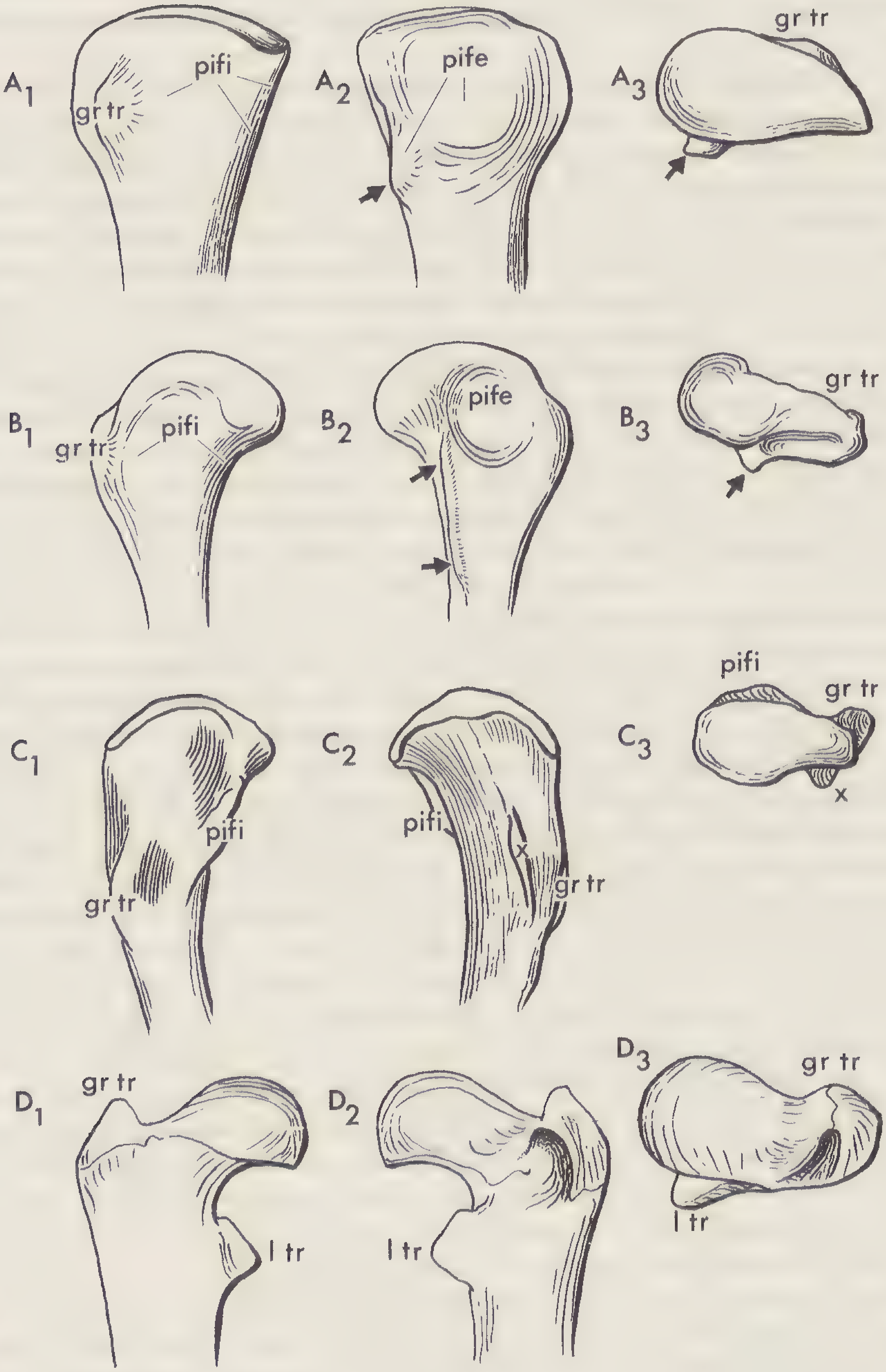

FIG. 54. Proximal ends of the femora of A, *Dimetrodon*; B, *Cynognathus*; C, a whaitsid therocephalian; D, *Didelphis*. C after Parrington, 1961: fig. 7 and a cast of this specimen. Subscript 1, dorsal views; subscript 2, ventral views; subscript 3, proximal views. Arrows indicate the anteroventral trochanter, variously considered the (reptilian) trochanter internus or (mammalian) lesser trochanter. Abbreviations: *gr tr*, greater trochanter; *l tr*, lesser trochanter; *pifi*, pubo-ischio-femoralis internus insertion; *pife*, pubo-ischio-femoralis externus insertion; *x*, the supposed trochanter internus as identified by Parrington. Not to scale.

of pubo-ischio-femoralis internus insertion (*pifi*, Fig. 54C). The femur of a scaloposaurid bauriamorph bears the same features as the whaitsid femur. Both forms would appear to substantiate Romer's (1924) claim that the internal trochanter migrated posteriorly in therapsids and its original position was occupied by a lesser trochanter that migrated ventrally from the anterodorsal aspect of the shaft.

However, there are several objections which may be raised against Parrington's interpretation. First, there is no evidence that the figured femora represent forms ancestral to cynodonts. The bauriamorph from the Early Triassic is certainly too late and the whaitsid from the Late Permian is at least contemporaneous with the earliest cynodonts. The phylogenetic relationship of the therocephalians and bauriamorphs to the cynodonts is by no means established. Parrington recognized this fact in his diagrammatic representation of therapsid evolution; the therocephalians are tentatively considered to have been derived from titanosuchids and bauriamorphs from the therocephalians, but the question of cynodont ancestry is left open.

A second question raised by Parrington's hypothesis is whether the figured femora represent a morphologically intermediate type between primitive and advanced therapsids or whether the femora are morphologically specialized. In view of the doubtful relationship of the whaitsids and scaloposaurids to cynodonts there is no substantial proof that the femoral trochanter morphology is intermediate. The case can be argued that whaitsid and scapolosaurid femora are peculiarly specialized and the critical question here concerns the identification of the internal trochanter. According to Parrington the internal trochanter lies beneath and is more or less a direct continuation of the greater trochanter. However, Parrington's internal trochanter might simply represent a ventral enlargement of the greater trochanter. In this case the true internal trochanter is lost. This interpretation is made more plausible by the fact that a parallel development occurred in anomodonts; the internal trochanter of dinocephalians is reduced and is altogether absent in dicynodonts (Parrington, 1961: 291). But anomodonts did not develop a true lesser trochanter (i.e., a pubo-ischio-femoralis internus trochanter) that shifted from a primitive dorsal to a ventral position. Therefore the loss of the internal trochanter need not be directly related to the origin of a lesser trochanter. I find no convincing evidence to support the interpretation that the pubo-ischio-femoralis insertion on whaitsid and scaloposaurid femora was located in any other but the primitive anterodorsal position.

Even if Parrington's identification of the whaitsid and scaloposaurid trochanter internus is correct (i.e., *x* in Fig. 50C representing the pubo-ischio-femoralis externus insertion), the pubo-ischio-femoralis internus insertion in both forms retains only the dorsal part of its primitive position and shows no tendency toward ventral displacement. In fact the apparent restriction of the insertion to the dorsal surface might be interpreted as a specialization. In pelycosaurs the insertion is marked by an area of rugosity which covers both the dorsal and anterior (medial) aspects of the shaft (Fig. $54A_1$; see MCZ 1969, a *Dimetrodon* femur). According to Parrington's interpretation only the dorsal area of insertion is present in whaitsids and scaloposaurid femora.

There is no disputing the fact that the internal trochanter of reptiles is not the homologue of the mammalian lesser trochanter; it is clearly established that different muscles attach to each. The point of dispute is how the mammalian pattern arose. Romer's (1924) hypothesis of trochanter migration is based on an incorrect assessment

of the trochanter position in cynodonts and on the dubious view that the lesser trochanter position in monotremes is truly primitive. Parrington's attempt to further document Romer's hypothesis fails to demonstrate the probability of migration of the pubo-ischo-femoralis internus insertion. An alternate possibility remains, that an anteroventral trochanter has always been present on the femora of synapsids which were on or near to the line of mammalian ancestry and that the muscular relations of the anteroventral trochanter changed during the evolution of the mammalian locomotory system. In pelycosaurs the insertions of the pubo-ischio-femoralis internus extended to the anterior (medial) face of the anteroventral trochanter (Fig. $54A_1$) but not to its apex. The apex of the anteroventral trochanter was probably occupied by the pubo-ischio-femoralis externus as was the adjacent intertrochanteric fossa (Fig. $54A_2$). In mammals the obturator externus (the pubo-ischio-femoralis externus homologue) does not insert onto the anteroventral trochanter but is confined to the intertrochanteric fossa. The iliacus and psoas muscles (the pubo-ischio femoralis internus homologue) apparently have gained an insertion on the apex of the trochanter. The hypothesized shift in attachments is slight because the ilio-psoas homologue in pelycosaurs (pubo-ischio-femoralis internus) is interpreted to have inserted partly on the anterior aspect of the anteroventral trochanter (Fig. $54A_1$). This hypothesis requires no trochanter migration, disappearance or de novo origin for which there is no evidence in mammalian ancestry.

The hypothesized shift in the muscular relationships of the anteroventral trochanter appears to be related to basic changes in femoral orientation and excursion between early synapsids and mammals. The obturator externus and ilio-psoas will be considered separately in this regard. The pubo-ischio-femoralis externus (or obturator externus) of pelycosaurs was probably a relatively large adductor acting across the ventral aspect of the hip joint. Adduction of the femur among early synapsids was most likely the principle mechanism for elevating the body off the ground during locomotion. In mammals the adductor function and orientation of the obturator externus appears to have been retained essentially unchanged. However, less adductor effort to maintain an elevated body position would be required by a mammalian posture with femora in a more or less parasagittal plane than by an early synapsid posture with femora in a more or less horizontal plane. For this reason it appears that the obturator externus, among other adductors, plays a less important postural role in mammals than in early synapsids. The relative diminution of the interochanteric fossa and the interpreted recession of the obturator externus from the anteroventral trochanter are here constructed as sequelae to the relative decrease in functional importance of the obturator externus for mammalian posture.

The pubo-ischio-femoralis internus of pelycosaurs is interpreted as having taken origin from the medial surface of the pubis and as having inserted onto the anterior aspect of the anteroventral trochanter and the dorsal aspect of the proximal shaft (*pifi*, Figs. 50A, $54A_1$). The origin and insertion lie at approximately the same horizontal level. Thus reconstructed, this muscle is likely to have functioned as a femoral protractor by swinging the femur forward in a more or less horizontal arc. The homologous musculature in mammals, the ilio-psoas group, also functions as a femoral protractor (or, in more common usage, flexor of the thigh) but with the important difference that femoral excursion is in a nearly parasagittal rather than a horizontal plane. The apparent dor-

sal migration of the ilio-psoas group from its primitive attachment to the pubis (as the pubo-ischio-femoralis internus) is explicable in terms of introducing an upward component to femoral flexion. The shift of ilio-psoas insertion onto the anteroventral trochanter appears to be related to the development of an inflected femoral head and the resultant repositioning of the mechanical axis. In mammals the mechanical axis passes through the femoral head and between the tibial condyles (Fig. $55A_1$). If the ilio-psoas had remained in a position analogous to that in pelycosaurs—on the anterior and dorsal aspect of the proximal shaft (Fig. 55B)—the insertion would lie lateral to the mechanical axis. Such an arrangement would engender a substantial rotational component to ilio-psoas action and the result of both flexion and rotation might appear as in Figure 55B. However, the migration of ilio-psoas insertion onto the apex of the lesser trochanter eliminates any major rotational component because the insertion lies approximately on the mechanical axis. Flexion alone results. Although there has been longstanding controversy over the possible rotational actions of the ilio-psoas, electromyography in humans, at least, has demonstrated that no rotational components exist (Basmajian, 1967: 206–209). Insertion of the ilio-psoas onto the lesser trochanter thus appears to be an arrangement to produce flexion of the thigh without rotation—the simplest movement to advance the femur in a nearly parasagittal plane.

In conclusion, it seems likely that there has always been an anteroventral trochanter (an internal trochanter or a lesser trochanter) in synapsids that were on or close to the line of mammalian ancestry. In the more primitive forms the trochanter was associated primarily with the pubo-ischio-femoralis externus and to a lesser extent with the pubo-ischio-femoralis internus. In later forms the pubo-ischio-femoralis internus became inserted primarily on this trochanter in conjunction with the requirements of a more mammalian posture and femoral movement. It cannot be determined with certainty in which pre-mammalian form or forms the pubo-ischio-femoralis internus occupied it exclusively. It would seem that this shift would be accomplished by the development of the mammalian form of pelvis. The earliest pelvis of a mammalian pattern is

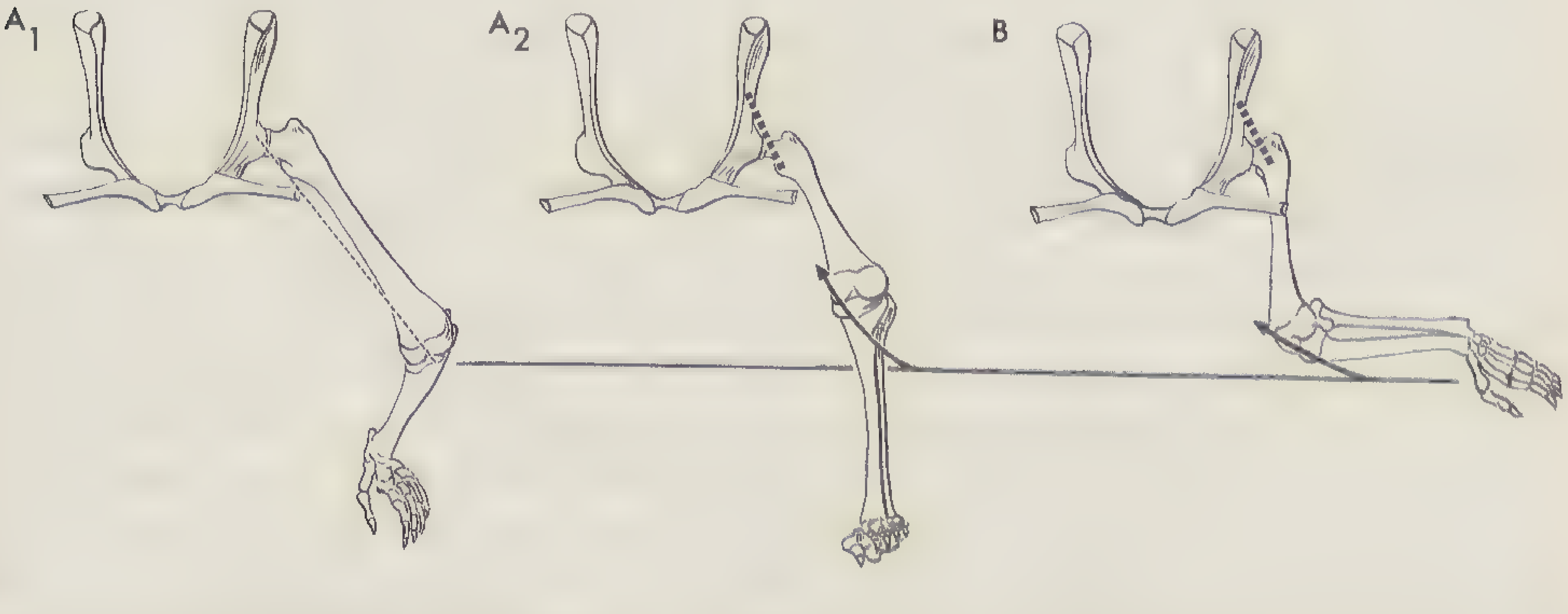

FIG. 55. Pelvis and hindlimb of a mammal in anterior view to demonstrate the action of ilio-psoas musculature. Insertion of this musculature on or near the lesser trochanter flexes the femur from a position in A_1 to a position in A_2. If the ilio-psoas musculature had retained its primitive insertion on the dorsum of the femur, flexion would be accompanied by counterclockwise rotation, resulting in the bizarre position illustrated in B. The horizontal line provides a plane of reference. Thick dashed line indicates position and insertion of ilio-psoas; thin dashed line indicates position of the mechanical axis of the femur.

known among the tritylodontids (e.g., *Oligokyphus*; Kühne, 1956) which are derivatives of advanced cynodonts but are not mammalian ancestors. In these forms the lesser trochanter has assumed a recognizably mammalian shape.

Tibia (Figs. 56, 57)

MATERIAL. With the exception of size and minor proportional differences, cynodont tibiae are very much alike. The tibia in *Thrinaxodon* is known from specimens listed by Brink (1954) and from BPI 376 and BPI 287. The most complete of available specimens is SAM K.1395.

Tibiae of *Cynognathus* and *Diademodon* are preserved in two collections (BPI 1675; NMB C.2696). The two genera cannot be distinguished on the basis of tibial morphology. The supposed tibia of *Gomphognathus* (=*Diademodon*) *kannemeyeri* (SAM 977) may be either *Diademodon* or *Cynognathus*.

A crushed right tibia (DMSW R. 189), possibly but not certainly referable to *Diademodon*, was recovered in association with a right fibula. This is one of the few specimens in which it is possible to examine the crural elements of the same individual.

Parrington (1934) described fragmentary tibiae from a specimen (UMC R.2722) supposed to be *Galesaurus* but which, lacking associated cranial remains, could just as probably be *Thrinaxodon* (see above p. 62).

MORPHOLOGY. The shaft of the cynodont tibia is anteroposteriorly flat and bowed slightly medially (Figs. 56, 57). The proximal end expands laterally and somewhat anteriorly to support a large articular surface. The distal end expands in a similar fashion but less extensively. As a result of this expansion the lateral margin of the tibia is markedly concave while the medial margin is only slightly so. Likewise the anterior (extensor) surface is somewhat concave while the posterior (flexor) surface is straight.

The proximal articular surface, irregularly oval in outline, bears two oval facets for articulation with the femoral condyles (*pr ar f*, Fig. 56A,C). Both facets are slightly concave and are separated by a low ridge running posteromedially. The anteromedial facet, inclined anteromedially with its axis transverse, contacts the medial (smaller) femoral condyle. The laterally inclined lateral facet, with its axis running posteromedially, contacts the lateral (larger) femoral condyle. The posteromedial corner of the articular surface is convex and is continuous with the ridge separating the condyles. A tubercle projecting from the anteromedial margin of the articular surface (*tb q*, Fig. 56A) may represent the insertion of quadriceps musculature; a similar and apparently homologous tubercle occurs on pelycosaur tibiae (Romer and Price, 1940: 156). Medial to this tubercle is another smaller tubercle (*tb*, Fig. 56A) which is absent, or at least unossified, in galesaurids. Between the two tubercles the rim of the proximal facet is emarginated and pulley-like. Possibly a ligament or tendon crossed this point between the femur and the lower leg.

The tibial shaft is flattened anteroposteriorly and is thus clearly divided into extensor (anterior) and flexor (posterior) surfaces. The extensor surface as a whole is rather flat except for a ridge which transverses the shaft obliquely from medial to lat-

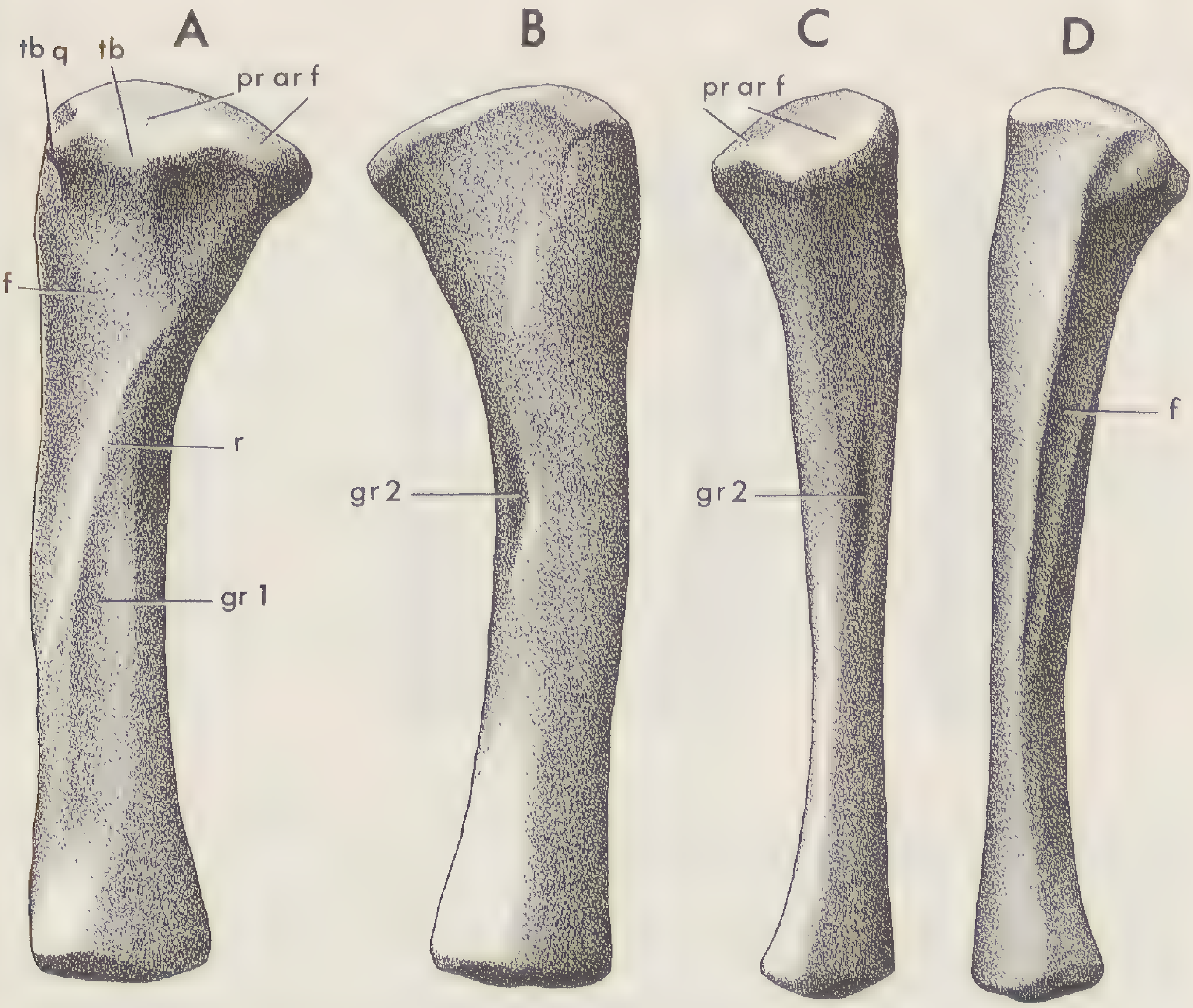

FIG. 56. Left tibia of cf. ?*Cynognathus* (?*Diademodon*), NMB C.2696, in A, anterior; B, posterior; C, lateral; D, medial views. X2/3. Abbreviations: *f*, fossa possibly representing the origin of a pedal dorsiflexor; *gr 1*, *gr 2*, grooves of uncertain function; *pr ar f*, proximal articular facets; *r*, ridge of uncertain function; *tb*, tubercle of uncertain function; *tb q*, tubercle possibly for quadriceps insertion.

eral aspect (*r*, Figs. 56A, 57A) Proximomedial to this ridge the extensor surface bears a shallow but distinct fossa of uncertain function (*f*, Figs. 56A,D, 57A); possibly it represents the origin of a pedal dorsiflexor. Both fossa and ridge disappear upon reaching the medial margin of the shaft which separates extensor and flexor surfaces. Undoubtedly both features are related to extensor muscle attachment, but it is uncertain which muscle or muscles are most likely to have been involved. The distal half of the extensor surface is flat except that in well-ossified specimens a slight groove can be detected (*gr 1*, Fig. 56A). This groove runs distally from the midpoint of the oblique ridge and extends to the distal end where it is terminated by the swelling of the distal articular facet rim. The only muscular association with this groove might possibly be a short digital extensor, but the usual origin for such a muscle in recent tetrapods is fibular and thus a proposed tibial origin for cynodonts is suspect.

Flexor and extensor surfaces adjoin medially along a sharply defined ridge (Figs. 56D, 57C). In well-ossified tibiae a tubercle occurs on the proximal end of this ridge. Flexor and extensor surfaces are separated laterally along their proximal half by a well-

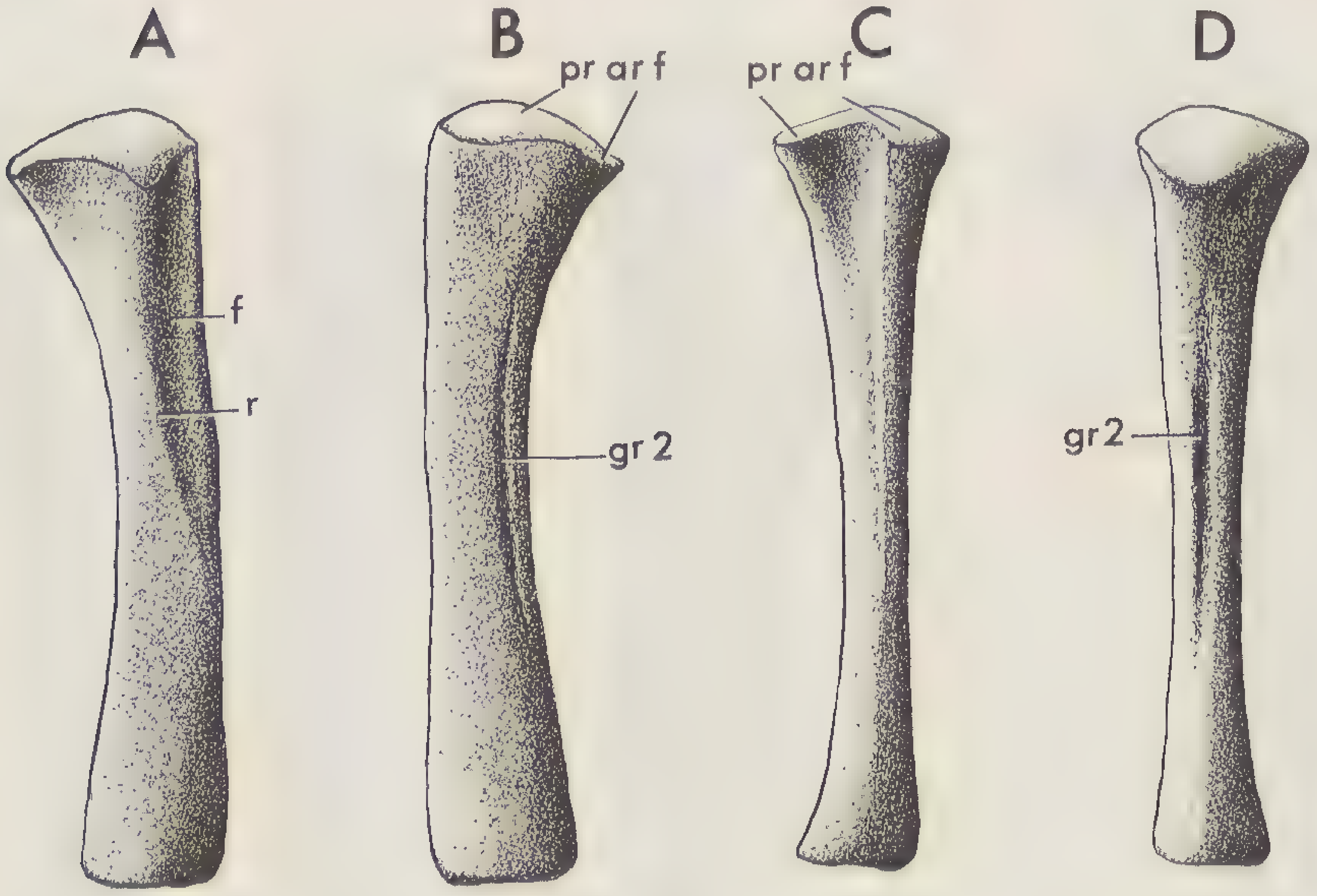

FIG. 57. Right tibia of *Thrinaxodon*, SAM K. 1395, in A, anterior; B, posterior; C, medial; D, lateral views. X2. Abbreviations as in FIG. 56.

rounded part of the shaft (Figs. 56C, 57D). Distally the separation of flexor and extensor surfaces is more sharply defined.

The flexor surface is more or less straight from end to end but is convex mediolaterally. A deep, longitudinal groove is incised in the lateral side of middle of the shaft (*gr 2*, Figs. 56B,C, 57B,D). This groove, undoubtedly representing a muscular attachment, extends farther proximally than distally and is deepest at about the shaft midpoint. The groove is relatively longer and deeper in galesaurids than in larger cynodonts.

The distal end of the tibia is terminated by a flat, oval facet at right angles to the shaft axis. In the best preserved specimens this facet appears to be slightly convex although the articular cartilage may have formed a surface of somewhat different curvature. The apparent presence of apposing convex surfaces in the cynodont ankle joint (the other being the bulbous astragalar facet) is a peculiarity not easily explained.

FIBULA (Figs. 58, 59)

MATERIAL. Fibulae are the least well known of cynodont long bones. With very slender shafts and poorly ossified extremities they are usually disarticulated and damaged. Disassociated fibulae of *Cynognathus* and *Diademodon* are known from two collections (BPI 1675; NMB C.2701). A fibula (DMSW R.190), probably but not certainly referable to *Diademodon*, is one of the very few specimens associated with a tibia (DMSW R.189) from the same individual. Seeley (1895b: 148) described a

fibula referable to *Tribolodon frerensis.* This specimen could not be located and Seeley's description and figure are inadequate for purposes of comparison. *Thrinaxodon* fibulae are preserved in BPI 287, BPI 376, NMB C.373, but only in SAM K.1395 are they completely freed of matrix.

The BPI 1675 collection, in which both *Diademodon* and *Cynognathus* are represented, preserves two types of fibulae which differ in a number of features. Since these fibulae are of approximately the same size the differences are probably not due to ossification but may be generically related. If so, this is a unique occurrence of major dissimilarity in the postcranial skeleton of these two genera (insofar as known). Of course it is still not possible to identify generically the fibular types. For convenience they are referred to as fibular type I and type II (BPI 1675).

The orientation of cynodont fibulae will remain in doubt until more complete, articulated material is recovered. Only SAM K.1395 preserves the tibia and fibula in what is probably an approximation of their true positions relative to each other (Fig. 59). Typically, however, this *Thrinaxodon* fibula is poorly ossified and cannot be compared with absolute certainty to those of larger cynodonts. The cynodont fibula is very much modified from the pelycosaurian fibula, unlike other limb bones, and therefore comparison between the two establishes nothing in terms of orientation.

MORPHOLOGY. The slender fibular shaft is slightly expanded at each end and bowed laterally. The proximal end with the articular facet for the femur is usually poorly ossified but may be reconstructed from DMSW R.190 and DMSW R.192. The articular facet for the humerus appears to have been round and a little convex. As preserved in these specimens it faces medially and slightly dorsally. From the adjoining surface of the proximal end a prominent flange projects posteriorly (*fi fl*, reconstructed in Fig. 58C,D). This flange may have taken part in the femoro-tibial articulation but more probably served as a musculotendinous process. Presumably the flange is homologous with the greatly expanded head of the monotreme fibula to which attaches part of the gastrocnemius, popliteus, flexor fibularis, tibialis posterior, flexor tibialis and peroneus longus muscles (Lewis, 1963). However, the unusual size and extensive muscular relations of the fibular head in monotremes is no doubt a specialization.

The shaft at the proximal end is three-sided and thus triangular in cross-section. A sharp ridge descends from the proximal end along the medial aspect (*m r*, Fig. 58C). In some specimens (type I, BPI 1675) the ridge terminates between the first and second quarters of the shaft, as in Figure 58C, while in others (type II) it is continuous with a ridge along the posteromedial aspect of the shaft. This represents a major difference between the two fibulae because in type I the ridge extends toward, but does not reach, another longer ridge along the anteromedial aspect of the shaft (*a r*, Fig. 58C), whereas in type II it is continuous with a second ridge (also present on type I, *pm r*, Fig. 58C) along the posteromedial aspect.

The medial surface of the shaft, narrow proximally, gradually widens distally (Fig. 58C). The distal part is flat, with a slight longitudinal convexity just below the shaft midpoint. The flat area is bounded by two long ridges (*a r*, *pm r* mentioned above). The more prominent anteromedial ridge reaches the distal end of the bone (Fig. 58A) and in type I is split near its proximal end (Fig. 58C). In type II the anteromedial

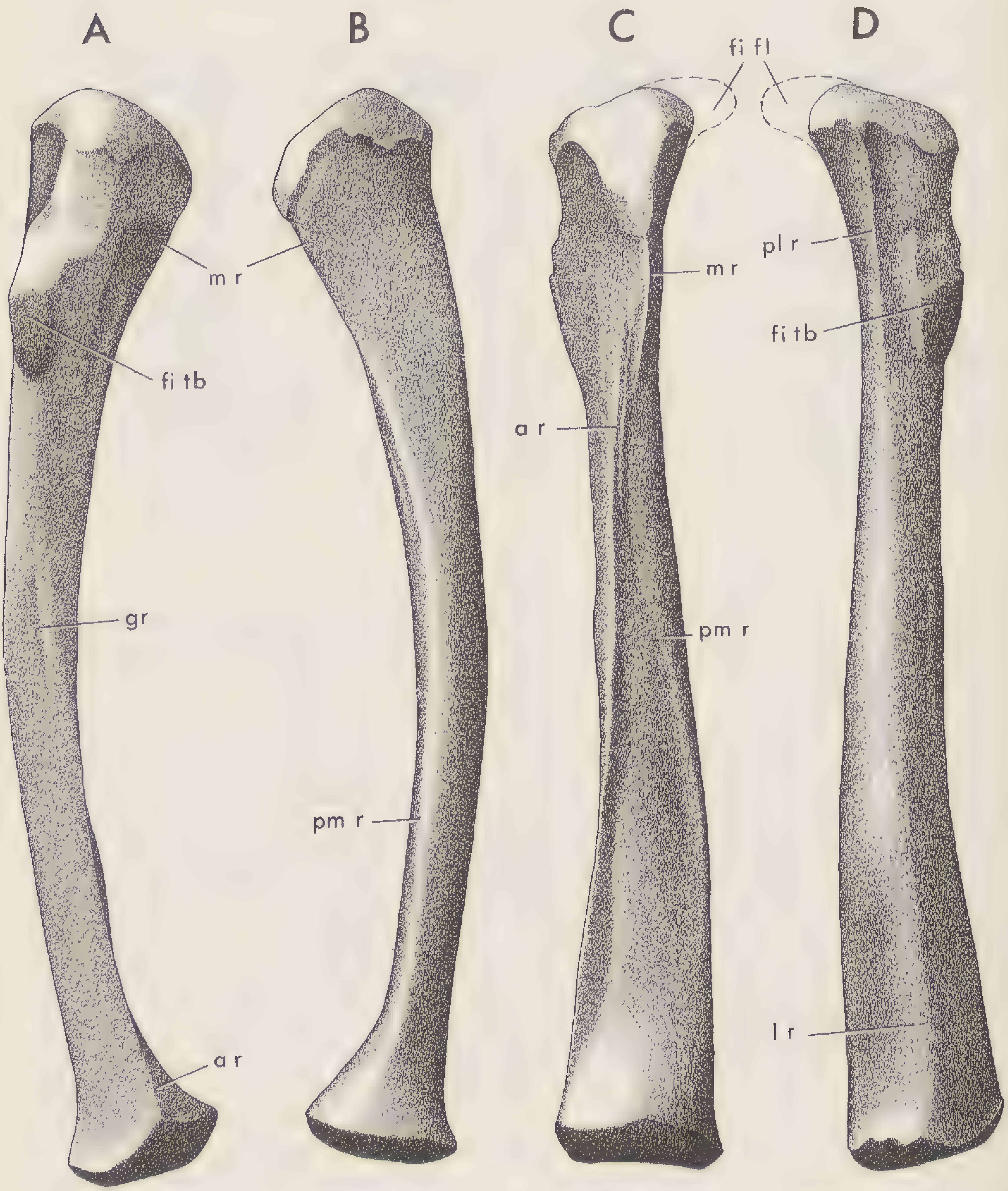

FIG. 58. Right fibula of cf. ?*Cynognathus* (?*Diademodon*), BPI 1675, in A, anterior; B, posterior; C, medial; D, lateral views. X1. Outline of proximal end reconstructed from DMSW R. 190 and DMSW R. 191. Abbreviations: *a r*, anteromedial ridge; *fi fl*, fibular flange; *fi tb*, fibular tubercle; *gr*, groove of unknown function; *l r*, lateral ridge; *m r*, medial ridge; *pl r*, posterolateral ridge; *pm r*, posteromedial ridge.

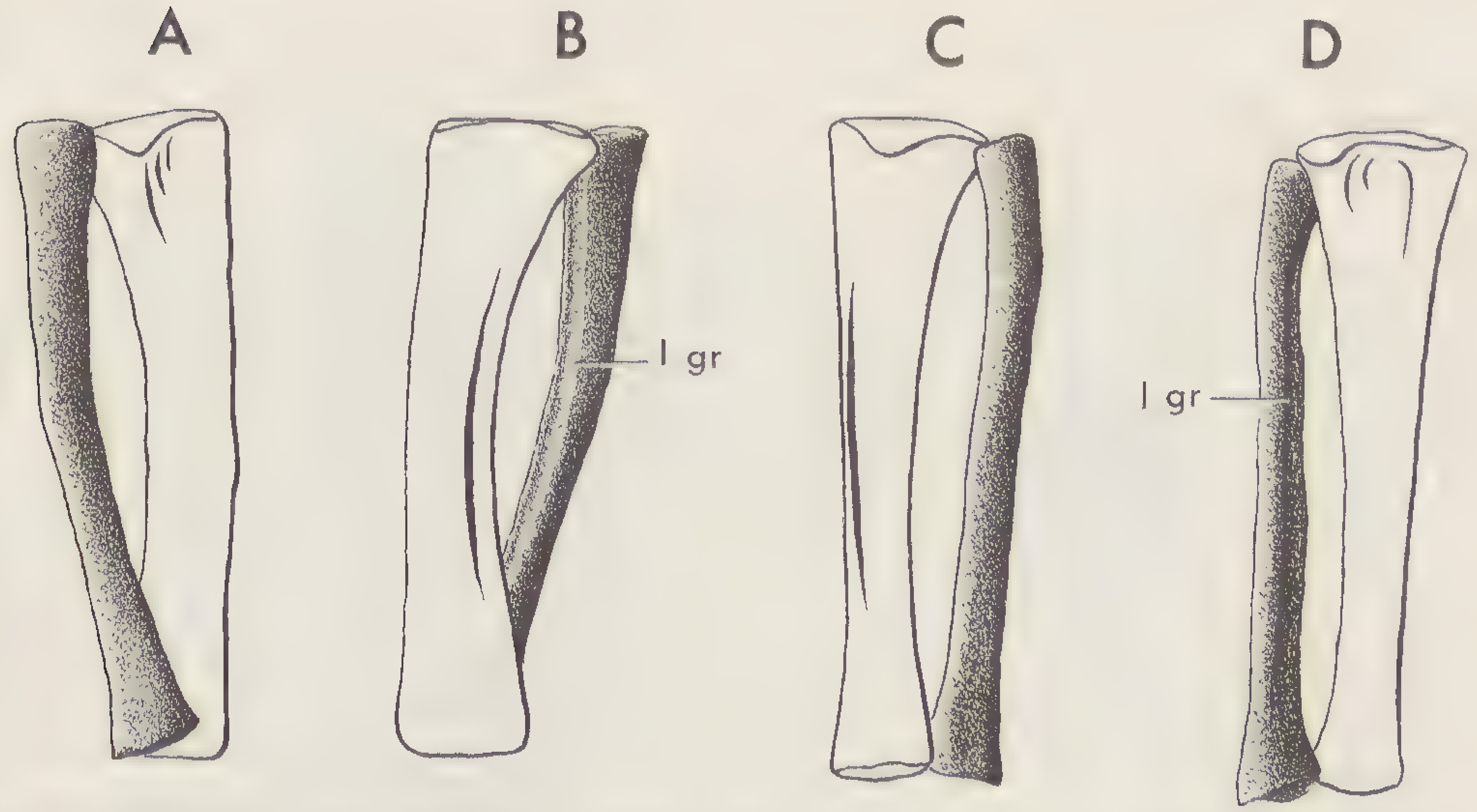

FIG. 59. Right fibula of *Thrinaxodon*, SAM K. 1395, associated with a tibia. A, anterior; B, posterior; C, lateral; D, medial views. X1. Abbreviations: *l gr*, groove presumed to be homologous with the space between *a r* and *pm r* in FIG. 58.

ridge also reaches the distal end of the shaft but bears a prominent flange in place of the split in the proximal end. The posteromedial ridge is less prominent and does not reach the distal end of the shaft in either type I (Fig. 58B) or type II.

In *Thrinaxodon* (Fig. 59) none of the foregoing features can be identified with certainty because of poor ossification. However, the medial surface of the shaft is incised by a longitudinal groove bounded on either side by distinct ridges (*l gr*, Fig. 59B,D). These ridges may represent the anteromedial and posteromedial ridges on the fibulae of larger cynodonts. The shaft is bowed laterally as in larger cynodonts but no further comparisons can be confidently made on the basis of available material.

It was noted above that the proximal end of the fibular shaft in larger cynodonts was triangular in cross-section, the medial angle being formed by a ridge (*m r*). In type I the other two angles of the proximal shaft are occupied by a posterolateral ridge (*pl r*, Fig. 58D) and a large anterolateral tuberosity (*fi tb*, Fig. 58A,D). In type II the posterolateral ridge is comparable but the tuberosity is merely a short, low flange.

In both types I and II a shallow groove is incised in the middle of the shaft along its anterior aspect (*gr*, Fig. 58A).

The distal end of the shaft is also triangular in cross-section but the triangle is oriented differently from that of the proximal end. Two angles are defined by the anteromedial and posteromedial ridges described above (Fig. 58A,B) and the third occurs as a lateral ridge (*l r*, Fig. 58D) which is confined to the distal half of the shaft.

The distal articular surface of the fibula is invariably poorly ossified. In one specimen of *Thrinaxodon* (SAM K.1395) and in type I the facet appears to be relatively flat. The former is oval in outline; the latter is piriform with its attenuated end beneath the terminus of the anteromedial ridge. It is unlikely that the distal end as preserved reveals much of the true shape of the articulating distal facet for tarsal contact.

Pes (Figs. 60–62)

MATERIAL. The only complete pes available for study is that of an unidentified cynodont (BMNH TR.8) from the Middle Triassic Manda Formation of Tanzania. Associated with this specimen are a complete femur, most of the pelvis, and part of the lumbar series which displays ribs similar to *Cynognathus* and *Diademodon*. Cranial material preserved with this specimen indicates a generic assignment of either *Aleodon* or *Scalenodon* (A. W. Crompton, personal communication).

Various elements of the pes are known from *Thrinaxodon*. In BPI 376 the plantar aspect of the right pes is exposed, revealing an incomplete set of metapodials (but no mesopodials). Disarticulated tarsalia (SAM K.1395) are preserved with other *Thrinaxodon* specimens. Broom (1932b: 270) figured a complete *Thrinaxodon* pes but in such a diagrammatic manner that its accuracy is questionable. The specimen on which the figure was based is apparently lost. Invariably *Thrinaxodon* tarsal bones are poorly preserved and thus appear to be more dissimilar to the tarsals of larger cynodonts than they probably were in life.

Isolated ?tarsal (?carpal) elements of *Cynognathus* or *Diademodon* are preserved together in one collection (BPI 1675) but are not sufficiently numerous or distinct to make generic separation possible. None of the readily recognizable tarsal bones (calcaneum, astragalus) are present. Apparently this limited sample contains only distal tarsal elements, as well as distal carpal elements.

The pes associated with an almost complete skeleton of *Diademodon* sp. (USNM 23352) is composed of rather poorly preserved bone in hard, tenacious matrix. Complete preparation is therefore impossible without further damage to the specimen. A sufficient amount is exposed to show that in all dimensions the hindfoot was considerably smaller than the forefoot (compare Fig. 34A with 34B), a feature which is probably related to the disproportionately large size of the head (see Brink, 1955: fig. 7). Brink's reconstruction of this genus incorrectly depicts the hindfoot as being slightly larger than the forefoot which is a common condition among terrestrial tetrapods.

Finally, there is an excellently preserved, isolated calcaneum (DMSW R.191) of an unidentified cynodont; according to the D.M.S. Watson catalogue it is probably referable to *Diademodon* sp. The specimen has been cleared of matrix and reveals details not seen elsewhere.

The following description of the cynodont pes is based primarily on the Manda cynodont (BMNH TR.8).

MORPHOLOGY. The cynodont calcaneum is distoproximally elongate and dorsoventrally compressed (Figs. 60A,C,D, 61). In lateral view its outline is arched, being slightly concave ventrally and convex dorsally (Fig. 61C,D). A prominent, rugose tuber calcis (*tb c*) composes almost one-third the length of the bone and is directed posteroventrally. Much of the remaining anterior two-thirds of the dorsal surface is flat except that the lateral margin is reflected dorsally (Fig. 61A). In DMSW R.191 a shallow sulcus crosses the dorsal surface obliquely from the anteromedial edge (*s'*, Fig. 61A).

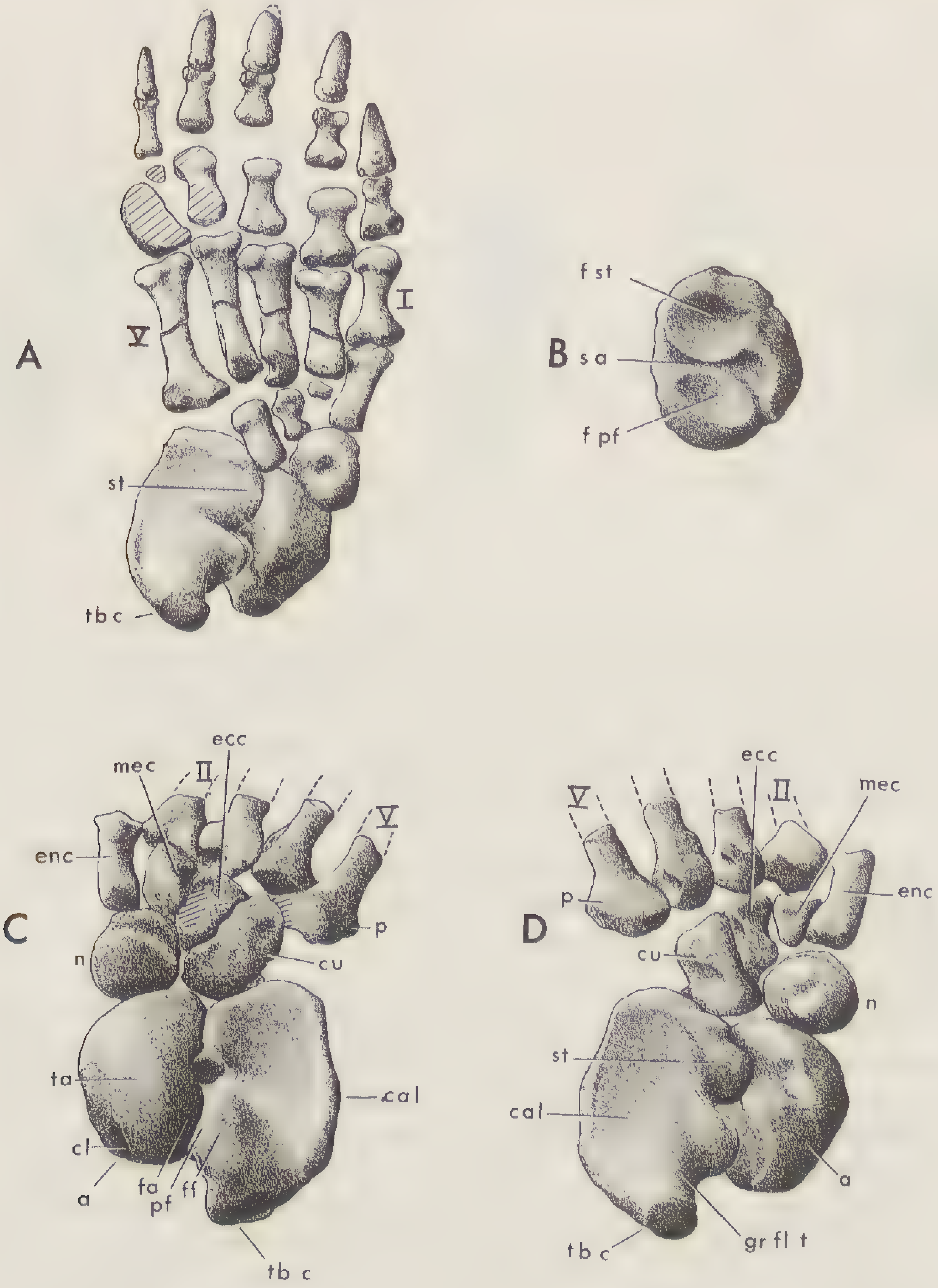

FIG. 60. Right pes of a Middle Triassic cynodont, BMNH TR.8, possibly referable to ?*Aleodon* or ?*Scalenodon*. A, plantar view of complete pes in situ, X1.2. B, ventrolateral view of the astragalus to show the two facets for articulation with the calcaneum, X1.6. C,D, dorsal and ventral views of the tarsus after further preparation, approx. X1.6; the calcaneum and astragalus have been reset to their correct positions relative to each other, but the other tarsals and metatarsal heads remain as found. Abbreviations: Roman numerals designate metatarsals; *a*, astragalus; *cal*, calcaneum; *cl*, cleft in astragalus of unknown function; *cu*, cuboid; *ecc*, ectocuneiform; *enc*, entocuneiform; *fa*, fibular facet of the astragalus; *ff*, fibular facet of the calcaneum; *f pf*, astragalar facet for the proximal calcaneal facet; *f st*, astragalar facet for the sustentaculum tali; *gr fl t*, groove for flexor tendon(s); *mec*, mesocuneiform; *n*, navicular; *p*, lateral process of metatarsal V possibly for insertion of short flexor and peroneal musculature; *pf*, proximal astragalar facet on the calcaneus; *s a*, astragalar sulcus; *st*, sustentaculum tali; *ta*, astragalar facet for the tibia; *tb c*, tuber calcis.

On the medial side of the calcaneum is a stout process that in dorsal view (Fig. 61A) appears rectangular in outline. The process lies almost entirely proximal (or posterior) to the transverse midline of the calcaneum. The process represents two separate articulations, one for the fibula (*ff*), the other for the astragalus (*pf*), but the delineation of the exact limits of the fibular facet is somewhat problematical. As here interpreted the fibula contacted at least the dorsal extremity of the rectangular process which has an oval, flat top (*ff*, Fig. 61A,D, Fig. 62B). The fibula may have also contacted part of the surface medially adjacent. This surface, which is rectangular in outline, bears one of the two calcaneal facets for the astragalus (*pf*, Figs. 61A, 62B). The orientation of this surface is dorsomedial (Fig. 61E). In BMNH TR.8 the medial process on the calcaneum does not project as far dorsally as in DMSW R.191, nor is the oval, dorsal extremity (*ff*) as clearly differentiated from the medially inclined surface (*pf*, Fig. 60C).

Anteroventral to the rectangular process is another process, the sustentaculum tali, which lies beneath the anterolateral aspect of the astragalus (*st*, Figs. 60A,D, 61A,B, D,E, Fig. 62B). This process represents an incipient morphological reorientation of the two proximal tarsals toward the mammalian condition in which the astragalus is supported by the calcaneum (see below). The rectangular process and the sustentaculum tali are separated by a sulcus (*s″*, Fig. 61D), evidently homologous with the intratarsal notch in pelycosaurs which Romer and Price (1940: 165) believed was for a "perforating artery". In DMSW R.191 the sulcus is more or less continuous with a previously described sulcus running obliquely across the dorsal surface (*s′*, Fig. 61A) and another sulcus extending for a short distance on the ventral surface (*s‴*, Fig. 61B).

On the medial side of the calcaneum between the rectangular process and the tuber calcis is a distinct groove for passage of a long flexor tendon (*gr fl t*, Fig. 60D). In DMSW R.191 the groove is apparently doubled by the occurrence of a low, dividing ridge (*gr fl t*, Fig. 61D).

In *Thrinaxodon* the calcaneum is oval by virtue of the fact that the tuber calcis was cartilaginous or not yet developed. The sulcus between the sustentaculum tali and rectangular process is distinct, but the processes themselves were apparently not ossified and are indicated only by indistinct tuberosities on the medial aspect of the calcaneum.

The astragalus is hemispherical with its flat surface directed ventrolaterally. On the anterior half of this surface is a large, oval facet for the sustentaculum tali (*f st*, Fig. 60B); posteriorly is a somewhat smaller, oval facet for the ventral half of the rectangular process of the calcaneum (*f pf*, Fig. 60B). The two facets are separated by a sulcus which represents the astragalar half of the tarsal sinus (*s a*, Fig. 60B). The dorsomedial half of the astragalus is bulbously convex (Fig. 60C) and the crural facets are not well preserved. The fibular facet is apparently represented by a small, flat surface on the posterolateral aspect of the convexity (*fa*, Fig. 60C) lying opposite the fibular facet on the calcaneum. A V-shaped notch is thus formed to receive the distal end of the fibula. The location of the tibial facet is more conjectural. There is no clearly defined facet on the dorsal surface of the astragalus which might represent the tibial contact. The most likely possibility is that the tibia articulated with the entire bulbous dorsal surface of the astragalus (*ta*, Fig. 60C). Since the crus is not preserved with these proximal tarsals there is no means of estimating how much of the dorsal surface was involved. The only noticeable feature on the dorsal aspect of the astragalus is a

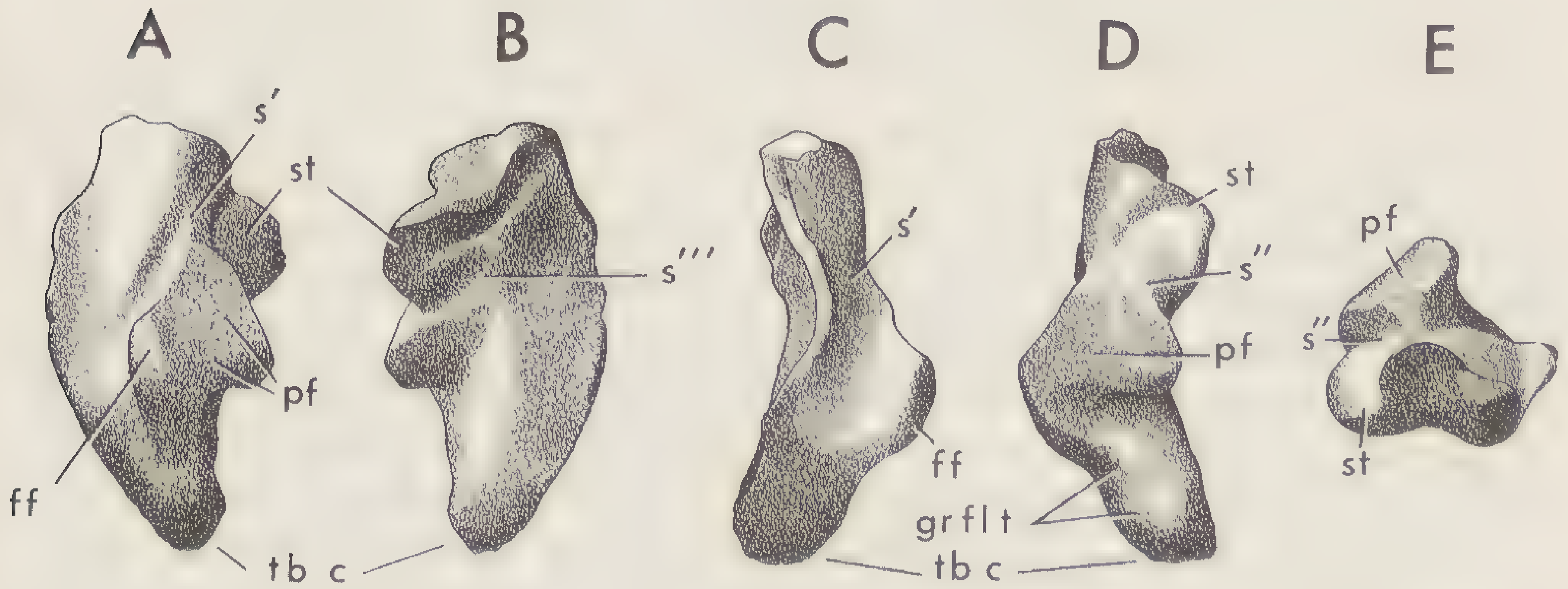

FIG. 61. Left calcaneum of a cynodont, DMSW R.191, possibly referable to *Diademodon*, in A, dorsal; B, ventral; C, lateral; D, medial; E, distal views. X1. Abbreviations as in FIG. 60 except: *s′*, *s″*, *s‴*, dorsal, medial and ventral parts, respectively, of a continuous calcaneal sulcus.

posteromedially located cleft of uncertain function (*cl*, Fig. 60C). An astragalus of *Thrinaxodon* also possesses this feature and is otherwise similar in form to that of the Manda cynodont.

The navicular is irregularly oval and bears a slight depression on its plantar surface (*n*, Fig. 60D). Its articular surface for the astragalus is shallowly concave. In addition to the astragalar contact it articulates with the first, second and third distal tarsalia (ento-, meso- and ectocuneiforms), and probably with the fourth distal tarsal (cuboid) as well. The nature and extent of these articulations is not certain because there has been some post-mortem displacement and because the articulating surfaces are not well preserved. Thus in Figure 60C and D the calcaneum and astragalus have been replaced in the correct position relative to each other but the navicular and distal tarsalia remain in approximately the same position in which they were found (Fig. 60A).

There are four distal tarsalia (Fig. 60C,D). The most medial (entocuneiform) is almost perfectly rectangular although its dorsal aspect is somewhat narrower than its ventral aspect. Distally it articulates with metatarsal I and apparently with a corner of metatarsal II. The second distal tarsal (mesocuneiform), the smallest of the tarsalia, is wedge-shaped by virtue of having a larger dorsal than ventral surface. Distally it articulates with metatarsal II; apparently it was accommodated medially and laterally by slight recesses in the adjacent distal tarsalia (I and III). Proximally it has only a short contact with the navicular. The third distal tarsal (ectocuneiform) is somewhat 8-shaped in outline, articulating distally with metatarsals III and possibly IV. The fourth distal tarsal (cuboid) is larger than the entocuneiform but has a rather similar rectangular shape. Distally it articulates with metatarsals IV and V, laterally with the ectocuneiform and navicular, and proximally with the astragalus and calcaneum. Like the other distal tarsals both the ectocuneiform and cuboid are wedged-shaped; they have broader dorsal than ventral surfaces (cf. Fig. 60C and D).

A complete set of metatarsals is known only from the pes of the unidentified Manda cynodont (BMNH TR.8). In this specimen the shaft diameters are all approximately the same, the greatest variability being in the shaft lengths and in the form of the proximal ends. The distoproximal lengths in millimeters are: I, 8.4; II, 10.2; III, 13.2; IV, 13.8; V, 14.6. The proximal ends of metatarsals I and II are mediolaterally expanded and bear rather symmetrical, trochlea-like articular surfaces. The proximal ends of III and IV, however, are mediolaterally compressed. Their articular surfaces are bulbous and are excavated laterally to permit articulation with the next (lateral) metatarsal (Fig. 60D). The proximal end of metacarpal V is mediolaterally expanded and bears a flat articular facet for the cuboid on its medial side. Laterally is a process (*p*, Fig. 60C,D) similar to that in many mammals where short flexor and peroneal musculature may have inserted. The distal ends of all of the metatarsals are similarly constructed; each is a trochlea-like facet with a vertical, median groove (Fig. 60A).

The digital formula of the Manda pes (BMNH TR.8) is 2-3-3-3-3. Broom (1932b: fig. 91) figured a *Thrinaxodon* pes having a count of 2-3-4-5-3 with the second phalanx of digit III and the second and third phalanges of digit IV reduced to intercalated discs. However, another pes of *Thrinaxodon* (BPI 376), in which the third and part of the fourth digit have been exposed, shows no trace of vestigial phalanges such as Broom figured. It is possible that they were lost post-mortem or during preparation but this in unlikely considering the pes is nearly articulated and the black bone is readily distinguished from the light-colored matrix. In view of Broom's unreliable interpretations of digital formulae in the carpus of *Thrinaxodon* and *Leavachia* (see above, p. 129 ff.) his statements concerning the pes are also suspect—especially because his figured specimen is apparently lost. While the question of pedal digital formulae in earlier cynodonts must remain open there is no doubt that the later forms attained the mammalian number.

The proximal phalanges are short and dumbbell-shaped with a rather sharp, median constriction. Their proximal articular surfaces are rectangular and vertical, their distal surfaces hemicircular and oblique to the vertical plane. The exception is the distal articular facet of the first proximal phalanx, which is unexpanded and bears a simple trochlea to accommodate the claw-bearing ungual phalanx. With a limited sample of proximal pedal phalanges known, there are no obvious morphological features, except relative size, which distinguish pedal from manual proximal phalanges.

The four penultimate phalanges are also indistinguishable from their analogues in the manus. The proximal articular facet is approximately rectangular and somewhat convex; the distal facet forms a trochlea for the ungual phalanx. There is a distinct morphological gradation from penultimate phalanx II which is robust and distinctly expanded at each end to that of V which is slender and very little expanded.

The ungual phalanges of BMNH TR.8 are dorsoventrally compressed and only slightly recurved. In the former respect they are different from other cynodont unguals which are more rounded and cone-like. Furthermore they are rather blunt—certainly not as sharply pointed as other cynodont unguals. This feature, however, could very well be a specialization of this unknown genus rather than a general cynodont character. The typical tuberosities for insertion of a long digital flexor tendon are present on the proximoventral aspect of each ungual.

3. FUNCTIONAL CONSIDERATIONS OF THE PES

Cruro-Pedal Joint

A discussion of the evolution of the mammalian cruro-pedal joint may conveniently begin with the pelycosaur tarsus which is sufficiently primitive to bear resemblance to the captorhinomorph pattern (Schaeffer, 1941b: 448-449). Romer and Price (1940) described the pelycosaur tarsus in detail and Schaeffer (1941b) discussed the pelycosaur tarsus in terms of function. Schaeffer stated that his functional interpretation is drawn largely from Romer's work but since no such detailed analysis can be found in Romer and Price's *Review of the Pelycosauria* the conclusions must be regarded as Schaeffer's. Schaeffer concluded that the long axis of the pelycosaur foot was directed forward during locomotion and that initially the body weight was transferred to the ground by the calcaneum and astragalus. Subsequently the weight was shifted to the metatarsals as the posterior part of the foot was lifted off the ground. Such a functional system, according to Schaeffer, must have generated "tension-compression stresses of considerable magnitude" which were probably resisted by tarsal ligaments and associated musculature.

Schaeffer's interpretation is questionable only with regard to the orientation and functional role of the calcaneum and astragalus during the initial phase of each stride. An important feature to understanding hindlimb function is the nature of the cruro-pedal joint. Opposing articular surfaces of this joint in pelycosaurs are more or less flat; movement here was probably a limited range of flexion and extension. In order for locomotory forces to have been transmitted by the calcaneum and astragalus (even via a heel pad as Schaeffer suggests) and not by the more distal tarsals, the calcaneum and astragalus must have been close to and nearly parallel with the ground. Yet cruro-pedal joint movement was probably so limited that the crus would have also assumed a similar orientation. In such a posture the muscular effort to raise the crus (and thus initiate the propulsive phase of the stride) would tend to disarticulate the cruro-pedal joint because the forces would be directed parallel to the plane of the articular surfaces. In fact the cruro-pedal joint appears to be adapted to transmit forces largely perpendicular to its articular surfaces. For this reason the pelycosaur calcaneum and astragalus probably did not have a plantar contact during the initial phase of propulsion, but remained off the ground throughout the entire stride (Fig. 51A).

Schaeffer's contention that the pelycosaurian tarsus was subject to considerable stress during locomotion is important to understanding subsequent developments in therapsid and mammalian cruro-pedal joints. The weight borne by the hindfoot was transmitted from the crus to the distal tarsus and metatarsus via the astragalus and calcaneum. The tarsus and metatarsus formed an arc (concave forward) between the horizontal digits and the crus (lateral view, Fig. 51A). At the end of a step, with the crus in a vertical or near vertical position, the arc was most pronounced and the tendency to intertarsal dislocation greatest. As Schaeffer suggested, this inherent weakness

must have been offset by strong tarsal ligaments and muscles. However, the presence of strong ligaments must have also restricted the mobility of the pes to a limited range of flexion and extension.

Schaeffer (1941b: 449) stated that "not until the mammalian stage was reached, was a longitudinal tarsal arch created to counteract the stresses". This statement might be interpreted to mean that there was little or no functional evolution of the therapsid pes beyond the pelycosaurian condition. To the contrary, Schaeffer's studies (1941a, b) provide ample evidence of mammalian pedal features among therapsids. Of particular importance is the development of the plantigrade pes. Strictly defined, plantigrade posture is contact of the entire sole with the ground. In mammals a plantigrade posture involves plantar contact of the skin immediately beneath the calcaneal tuber. Among therapsids, however, the plantar surface of both the calcaneum and astragalus participated in support of the heel. Ultimately complete astragalar superposition removed the astragalus from plantar contact, thus creating a mammalian type of plantigrade foot (see below, p. 200). Derivation of a therapsid type of plantigrady from the pelycosaurian posture in which neither calcaneum nor astragalus had plantar contact involved: 1) distal displacement of the fibulo-tarsal articulation onto the dorsum of the calcaneum and astragalus and 2) lateral displacement of the tibio-astragalar articulation onto the dorsum of the astragalus. Displacement of the latter articulation is a trend begun among pelycosaurs and continued among therapsids (Schaeffer, 1941b: 449); in gorgonopsids of the lower *Tapinocephalus* zone both the fibular and tibial facets are already on the dorsum of the calcaneum and astragalus, respectively (Boonstra, 1965). The pes of a cynodont from the Manda Beds (BMNH TR.8) retains the dorsal cruro-pedal articulation developed among earlier therapsids. The functional significance of therapsid platigrady appears to relate to specialization of the cruropedal joint for increased flexion and extension. In pelycosaurs the intertarsal, tarsometatarsal and metacarpo-phalangeal joints probably all participated in pedal flexion and extension but were limited in their individual contribution to movement by ligaments. These ligaments, as suggested above, would have been necessary to reinforce the arcuate arrangement of foot bones (see lateral view, Fig. 51A) against bending moments generated by body weight and propulsive force. The relatively flat cruropedal articular surfaces are evidence that flexion and extension here were probably not much greater than at the intertarsal joints. The elevated posture of the proximal tarsus and the relatively small articular surfaces of the cruro-pedal joints almost certainly necessitated supporting ligaments that in turn restricted joint motion. In therapsids the plantar contact of the calcaneum and astragalus provided extrinsic stability to the proximal tarsus as the cruro-pedal joint became specialized for an increased range of flexion and extension. Concomitantly, the remaining tarsals no longer participated individually in flexion and extension but became functionally conjoined with the proximal tarsals to form a lever powered largely by the triceps surae. Specialization for this movement is further developed in mammals. The malleoli and their associated ligaments are major stabilizing features of the mammalian ankle joint, but malleoli are as yet unknown in any cynodont. The evolution of a plantigrade posture therefore appears to be a principal factor in stabilizing an increasingly mobile ankle joint that was evolving as part of a triceps surae-calcaneal tuber lever system.

Tarsus

The acid-prepared calcaneum and astragalus of BMNH TR.8 reveal several important features not previously known in cynodonts. These features represent incipient specializations toward a mammalian type of calcaneum and astragalus. First, the calcaneum is anteroposteriorly elongate, thus approaching the characteristic mammalian shape. Approximately half of its width is composed of a thin, lateral flange, the outline of which (seen in dorsal view, Fig. 62B) is straighter from front to back than that in primitive *Tapinocephalus* zone therapsids (see Boonstra, 1965 and 1966); the flange is apparently in the process of reduction. Its absence would result in proportions essentially similar to that of a mammalian calcaneum, although some mammals (e.g., *Didelphis*) retain a slight lateral shelf on the calcaneum.

A second important feature is the nature of the articulation between the astragalus and calcaneum. The two facets on the calcaneum (*st*, *pf*) are so aligned as to represent different parts of a single convexity which is divided by a calcaneal sulcus (*s″*, Fig. 61D). The opposing astragalar facets represent parts of a single concavity also divided by an astragalar sulcus (*s a*, Fig. 60B). Therefore the calcaneo-astragalar articulation is a shallow ball and socket joint with the possibility of more than the inversion-eversion movements that characterize this joint in mammals. More important than the intertarsal movement, however, is the support afforded by the calcaneum for the astragalus, for the astragalus actually overlaps the calcaneum. Although the opposing facets meet at angles of about 45° to the horizontal with the resultant tendency for the astragalus to dislocate medially, ligaments probably reinforced the articulation. The astragalus appears to have been supported as much by the calcaneum as by its own plantar surface. As a result, the plantar surface of the astragalus is reduced to a rather narrow surface in close proximity to the plantar surface of the calcaneum (Fig. 60D). This condition represents a stage in the evolution of the mammalian type calcaneo-astragalar joint in which the astragalus no longer has a plantar contact but is supported entirely by the calcaneum.

Schaeffer (1941a: 6) claimed that the pes of *Bauria cynops* (AMNH 5622) more closely approximates the mammalian condition than that of any other known therapsid and Romer (1956: 404) expressed a similar view. Schaeffer implied that the following characteristics of the bauriamorph tarsus are significantly mammal-like: the degree of "consolidation" or interlocking of tarsal bones, a "true, but weakly developed head" on the astragalus, and a transverse tarsal arch as indicated by a cuboideonavicular ligament, a wedge-shaped mesocuneiform (centrale 2) and a rudimentary sustentacular process. The cynodont tarsal material available to Schaeffer was inadequate, as his brief account (1941b: 454) testified. Now that more satisfactory material is known, a comparison of the supposedly advanced bauriamorph tarsus with that of cynodonts is possible.

Schaeffer's first criterion of comparison—"consolidation" or interlocking of tarsal bones—is unquestionably characteristic of mammalian tarsi. However as a criterion for estimating the degree to which a synapsid tarsus approached a mammalian pattern,

"consolidation" is a vague and subjective standard. As Schaeffer realized, specific intertarsal relationships are the most meaningful features for evaluating the evolution of a functionally mammalian tarsus. Furthermore, some intertarsal articulations in fossil and living reptiles are comparable in complexity to those in mammals. The apparent simplicity of some fossil reptilian tarsi may be largely the result of non-preservation of cartilage. Therefore no attempt will be made to evaluate the "consolidation" of the bauriamorph and cynodont tarsus; instead, specific intertarsal relationships will be considered.

ASTRAGALAR SUPERPOSITION

The calcaneo-astragalar articulation will be considered first as it represents one of the most important differences between the reptilian and mammalian tarsus. In mammals the astragalus lies between the calcaneum and the crus and has no plantar contact. From the reptilian position medial to the calcaneum the astragalus has moved laterally and dorsally to override and to be supported by the calcaneum. On the calcaneum of *Bauria* (AMNH 5622) there is a very small sustentacular process which extends beneath the astragalus. The calcaneal support of the astragalus was therefore incipient, but the astragalus in AMNH 5622 is apparently preserved in its correct position and lies almost entirely medial to the calcaneum as in reptiles. Calcaneal support of the astragalus in *Bauria* represents only a slight shift in weight distribution over the condition in primitive therapsids and pelycosaurs. Schaeffer (1941a: 4) stated that the calcaneo-astragalar articulation is "weak, as the articular facets of the related bones are narrow, plain surfaces." The calcaneo-astragalar articulation in cynodonts is more extensive than that in *Bauria*. The anteroposterior length of the sustentacular process approaches 30 percent of the calcaneal length in BMNH TR.8 which is comparable to mammalian proportions; in *Bauria* the length is about 20 percent. Secondly, the calcaneo-astragalar contact is almost as extensive as the plantar surface of the astragalus, evidence that much of the astragalar support was transferred to the calcaneum. The functional association of these tarsal bones is evident in Figure 60C and D and represents an advance over the narrow calcaneo-astragalar contact of bauriamorphs.

The evolution of the mammalian calcaneo-astragalar, or sub-talar, joint is illustrated diagrammatically in Figure 62. In pelycosaurs there are four features on the medial side of the calcaneum which are recognizable among cynodonts. On the distal end of the medial side there is a small articular facet on the astragalus (*st*, Fig. 62A). This calcaneal facet is continuous distally, at least as an osteological feature, with the calcaneal facets for the cuboid and fifth distal tarsal. Proximally this facet is separated from another facet (*pf*, Fig. 62A) for the astragalus by the intervening calcaneal sulcus (*cs*, Fig. 62A). The calcaneal sulcus is opposed by a similar astragalar sulcus, thus constituting a foramen. The proximal facet is confluent with a third and still more proximal facet (*ff*, Fig. 62A) which represents half of the articular surface for the fibula. Thus along the medial edge of the calcaneum there occur three facets and one sulcus. The two pairs of calcaneo-astragalar facets are quite flat and are evenly matched in

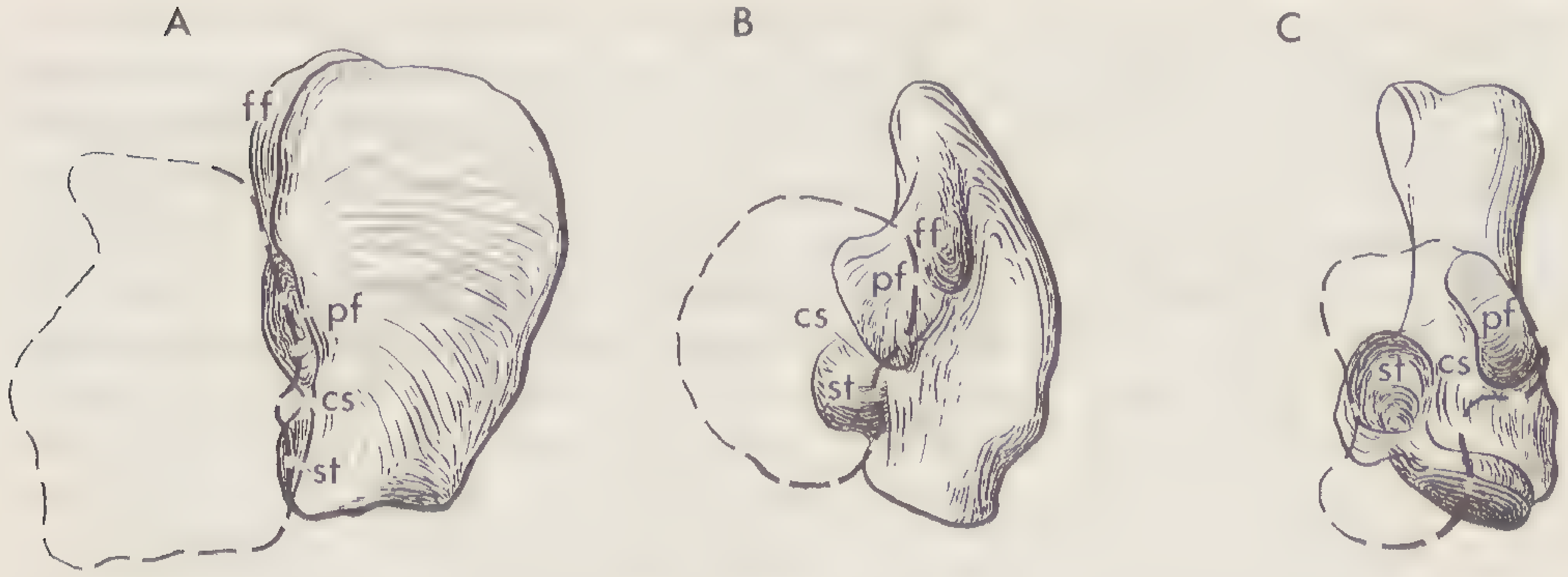

FIG. 62. Proximal tarsals of A, a pelycosaur (anterior view); B, a cynodont (dorsal view); C, a mammal (dorsal view). Astragalus outlined by dashed line; *cs*, calcaneal sulcus; *ff*, facet for fibular articulation; *pf*, proximal facet for astragalus; *st*, sustentacular facet, or its homologue, for astragalar articulation. Not to scale.

size; therefore, there could have been only a limited degree of movement between the astragalus and calcaneum. Furthermore, any substantial movement between these two tarsals would disrupt the fibular articulation which could be maintained only by a constant calcaneo-astragalar relationship.

In cynodonts (Fig. 62B) the same four features occur in linear sequence as in pelycosaurs although their orientation and position on the calcaneum is shifted. The distal facet (*st*) no longer faces medially, but is oriented dorsally and medially. This facet is supported by a sustentaculum tali which protrudes as a distinct process beneath the overlying astragalus. The calcaneal sulcus (*cs*) obliquely crosses the medial edge of the calcaneum. The proximal facet for the astragalus (*pf*) does not shift position as much as it changes orientation; like the sustentacular facet it faces dorsally as well as medially so as to support the astragalus from below. The fibular facet (*ff*) on the calcaneum displaces to the lateral side of the proximal astragalar facet; the primitive position of the fibular facet is now occupied by the tuber calcis. These modifications all relate to the calcaneal support of the astragalus. The more dorsal orientation of the astragalar facets on the calcaneum permit the astragalus to be partially supported by the calcaneum. The functional significance of astragalar superposition is discussed by Schaeffer (1941b: 455–457) and other authors cited by him. In simplest terms, superposition united the astragalus, which primitively transmitted most of the weight via the tibia, with the calcaneum; the calcaneum, through the development of a tuber, permitted the foot to function as a lever powered by triceps surae musculature and thus enhanced locomotory efficiency. With the growth of the tuber and the development of a plantigrade pes, the fibular facet is displaced from its primitive position at the proximomedial corner of the calcaneum.

In mammals (Fig. 62C) the trends evident among cynodonts are developed further. The sustentaculum tali and its astragalar facet (*st*) occur in the same position; the sustentaculum is a more robust feature. The proximal facet for the astragalus (*pf*) migrates further laterally and distally, and thus the astragalus loses any plantar contact of its own. The calcaneal sulcus (*cs*) which separates the two facets now runs obliquely across the dorsum of the bone instead of across its medial edge as in cynodonts and pelycosaurs. The fibular facet tends to be transferred to the astragalus as a

result of the narrowing of the calcaneum and the further reduction of the weight-bearing role of the fibula. The fact that the two astragalar facets on the calcaneum (*st*, *pf*) come to lie in a mediolateral relationship, contrasting to the proximodistal relationship in pelycosaurs, is probably related to the necessity for stabilizing the calcaneo-astragalar joint. Had astragalar superposition occurred by an equal amount of lateral migration on the part of both the sustentacular (*st*) and proximal (*pf*) facets, the sustentacular facet would lie directly distal to the proximal facet. Such an arrangement would obviously be prone to medial and lateral dislocation. In mammals the form of the calcaneo-astragalar joint tends to prevent such dislocation, despite the fact that the astragalus is supported only by a comparatively narrow calcaneum. First, the facets are in a mediolateral relationship, and second, their respective facet surfaces are inclined toward the midaxial line of the calcaneum. Both features tend to prevent the astragalus from dislocating to the medial or lateral side of the calcaneum.

During the pelycosaur-mammal transition the calcaneo-astragalar foramen apparently was modified for an entirely different function. In the tarsus of pelycosaurs and other primitive forms the foramen is formed by opposing grooves in the calcaneum (*cs*) and astragalus (Fig. 62A). Since neither bone is very thick, the foramen thus formed is only a short canal. Functionally, the foramen is usually regarded as representing the passage of a perforating artery (Romer and Price, 1940: 163; Schaeffer, 1941b: 430; Romer, 1956: 392), although no author cites evidence for a homologous structure in any living reptile. Whether arterial or venous, a vascular function for the foramen would seem to be indicated by the occurrence of sulci leading from both the dorsal and ventral openings in various pelycosaurs. The sulci are also present in cynodonts. Furthermore, well-preserved calcanei and astragali of pelycosaurs show that opposing grooves are evenly rounded, forming an almost perfectly circular foramen or sinus—a feature common to vascular or neurovascular foramina. There is no reason to doubt that the calcaneo-astragalar sinus of cynodonts is homologous with the foramen of pelycosaurs, for the sinus is bounded by the same two calcaneo-astragalar articulations which have only slightly shifted from their primitive position. However, the cynodont sinus is relatively longer than in pelycosaurs. In mammals the same two calcaneo-astragalar articulations are retained but their repositioning causes the sinus to run obliquely across the dorsum of the calcaneum. But more important, however, is the fact that in mammals there is no major vascular or nerve trunk traversing this sinus. Instead, the tarsal sinus is occupied primarily by a robust calcaneo-astragalar interosseous ligament, and secondarily by small neurovascular structures supplying the ligament and bone. This ligament is continuous distally and proximally with other cruro-pedal joint ligaments and serves the obvious function of reinforcing the calcaneo-astragalar joint from within. The vascular foramen of pelycosaurs thus appears to have been retained in mammals to meet mechanical rather than vascular requirements. The development of independent movement of the calcaneum and astragalus is likely to have introduced interference to the major vascular or neurovascular bundle passing in such close proximity to an active joint. With the course of this bundle transferred elsewhere, the sinus, filled with connective tissue, assumed a new function. A strong calcaneo-astragalar bond is necessitated by the fact that extension of the foot in locomotion is accomplished largely by muscular action on the calcaneum, whereas body weight is transferred to the calcaneum, and other tarsals, by the astragalus.

If the course of tarsal sinus evolution as outlined above is correct, then it would be of interest to know whether the cynodont tarsal sinus was vascular or ligamentous in function. Discrete sulci leading away from either side of the sinus (s', s''', Fig. 61A,B) opening are evidence that major vascular or neurovascular structures were still associated with the sinus. However, the walls of the sinus are asymmetric—not rounded as in a strictly vascular passage. The problem cannot be satisfactorily resolved without additional and better preserved material.

ASTRAGALO-NAVICULAR JOINT

A second characteristic feature of the mammalian tarsus is a rounded head on the astragalus that articulates with the navicular; the head proper is separated from the rest of the astragalus by a neck. Schaeffer (1941a: 4) claimed that the *Bauria* astragalus possesses a head but no neck, and implied thereby that this mammalian feature is incipiently differentiated. Reexamination of the specimen (AMNH 5622) reveals that Schaeffer's recognition of an astragalar head is difficult to justify. The anterior aspect of the astragalus articulates with the navicular and cuboid, contacting the former somewhat more extensively than the latter. In both cases the astragalar articular surface is slightly concave, not convex as is the astragalar head in mammals. The facets in *Bauria* are not borne on a process distinct from the astragalus, but occur flush with the main body of the bone. A "head", therefore, cannot be recognized. Neither can a head be recognized on the BMNH TR.8 astragalus. However, the navicular and cuboid facets on the astragalus of this cynodont appear to be flat or slightly convex and thus approximate the astragalar head of mammals more closely than that of *Bauria*.

TRANSVERSE TARSAL ARCH

One of the most characteristic features of a generalized mammalian pes is a transverse tarsal arch. In cross-section through the distal tarsus, the transverse arch is an arcuate arrangement of the wedge-shaped cuboid and three cuneiforms. The dorsal surfaces of these bones are larger than the plantar and thus adjacent bones act as keystones to form a dorsally bowed arch. The arch is maintained by joints, ligaments and muscular action; it serves the function of providing inherent structural strength while at the same time being sufficiently resilient to absorb shocks.

Schaeffer (1941a: 6) claimed that in *Bauria* "several features support the conclusion that there was a low transverse tarsal arch, namely, the indication of a well-developed cuboideo-navicular ligament, the wedge-shaped mesocuneiform, and possibly the rudimentary sustentacular process." The evidence for a strong cuboideo-navicular ligament is a knob-like process on the plantar surface of the cuboid. However, similar processes are common on the plantar surface of tarsals and may serve as points of tendon insertion or plantar support as well as intertarsal ligament attachment. The evidence for a cuboideo-navicular ligament is not conclusive. While such a ligament is

probably necessary for a transverse arch, its presence is not sufficient to demonstrate the existence of a transverse arch. Neither can the incipient development of astragalar superposition be construed as evidence of a transverse arch. In fact the only certain evidence of a transverse arch are wedge-shaped tarsals which result in a "keystone" arch. In *Bauria* only the mesocuneiform is perceptibly wedge-shaped. If there were any arching effect it must have been low, as Schaeffer correctly concluded. In the Manda cynodont (BMNH TR.8), however, all the distal tarsals are more or less wedge-shaped. The cuboid, ecto- and mesocuneiform each have a dorsal surface which is larger than the plantar surface and thus each acts as a keystone. The morphology of the entocuneiform is reversed with a dorsal surface slightly narrower than the plantar surface. The reversed wedging heightens the arching effect of the cuneiforms because the entocuneiform surface articulating with the mesocuneiform is inclined dorsolaterally. An analogous condition is best known in the human foot in which the "reversed keystone" shape of the entocuneiform serves the same function. The cynodont pes is unquestionably further advanced than that of *Bauria* with regard to developing a mammalian transverse tarsal arch.

TARSO-METATARSAL JOINTS

A fourth important aspect of the mammalian tarsus is the arrangement of the four distal tarsalia into a compact row of ossicles. Complex intertarsal and tarso-metatarsal articulations, reinforced by strong ligaments, create a cohesive but resilient structure. Partly correlated with this feature are the extensive articulations formed between the proximal ends of adjacent metatarsals. Such reinforcement probably serves to distribute forces more evenly across the tarsus and relieve stresses which might otherwise be borne by a single metatarsal. Both features are correlated with the mammalian tendency to narrow the plantar surface of the foot. In contrast, the primitive reptilian condition, approximated among pelycosaurs, is characterized by a broad, arcuate arrangement of the full complement of five distal tarsals (Fig. 51A). The digits tend to be splayed, the first and fifth diverging at angles of 60° or more (see Romer and Price, 1940: fig. 41). The proximal ends of the metatarsals are transversely expanded and among many forms the proximolateral corner of one metatarsal may overlie the proximomedial corner of the next lateral metatarsal. This articulation is a simple overlap and only superficially approximates the extensive intermetacarpal joints of mammals. In such primitive therapsids as dinocephalians the pes is essentially pelycosaurian with regard to these features; intermetatarsal contacts are not developed and the fifth distal tarsal is retained (see Boonstra, 1966). In more advanced therapsids, e.g., gorgonopsids, the distal tarsalia are more consolidated and reduce to four in number. However, the digits retain the splayed arrangement and the intermetacarpal contacts are only incipiently developed (e.g., *Lycaenops*; see Colbert, 1948).

With regard to the same features the pes of BMNH TR.8 represents the closest known approximation to the mammalian condition. The distal row of tarsalia forms a compact arch in which the intertarsal articulations are complex and snugly fitted. The metatarsals and digits are sub-parallel, as in mammals, and are not divergent as

in primitive synapsids. Most striking, however, are the complex articulations formed between the proximal ends of adjacent metatarsals. The proximomedial corner of the head of metatarsal V is received in a distinct groove on the proximolateral aspect of the metatarsal IV head (Fig. 60D). A similar pattern is repeated for metatarsals IV and III (Fig. 60C,D). The proximomedial side of the metatarsal II not only contacts metatarsal I but also the entocuneiform which is proximodistally elongate and extends farther distally than any other tarsal. This particular relationship is typical of mammals with a relatively generalized foot (e.g., *Didelphis*, *Taxidea*). The pes of *Bauria cynops* (AMNH 5622) is not sufficiently preserved or prepared to permit a confident determination of these details. It appears that the degree of proximal contact between metatarsals is less advanced than in BMNH TR.8. Furthermore, it is doubtful whether metatarsal II had as much contact with the entocuneiform as Schaeffer's reconstruction depicts. Whereas the cynodont pes definitely displays features that are recognizably mammalian, the bauriamorph pes as now known shows only the possibility that it may have closely approximated—but not attained—the cynodont level of organization.

CONCLUSIONS

No suite of postcranial features in the cynodont skeleton is so mammal-like as to constitute proof that mammals arose from known members of this group. Yet in many characters cynodonts are well advanced toward a mammalian pattern. Moreover, no known feature in the postcranial skeleton debars cynodonts from being the reptilian ancestors of mammals. Thus, the presence of many advanced, mammalian characters in the cynodont postcranial skeleton increases the probability that mammals were derived from a cynodont therapsid.

The principal conclusions of this study, aside from the descriptive text, may be summarized as follows:

1) The cynodont atlas-axis complex retains the same number of elements as in pelycosaurs and in reptiles generally. Morphologically, however, the cynodont pattern is incipiently specialized for atlanto-occipital flexion and extension and atlanto-axial rotation—the characteristic movements of the mammalian atlas-axis complex.

2) The evolution of the mammalian type of atlanto-occipital flexion and extension is characterized by i) a doubling of the condyles, ii) their subsequent displacement to the lateral margins of the foramen magnum, and iii) a migration of the foramen magnum from a position in the middle of the posterior aspect of the skull to a position on the posteroventral aspect. In all except the most primitive cynodonts the condyles are double. Condylar displacement to the mammalian position is incomplete, however, for they occur at the ventrolateral margins of the foramen magnum. The position of the foramen magnum is essentially mammalian. All of these changes are related to increasing the range of flexion-extension and concomitantly minimizing the resultant deformation of the spinal medulla.

3) The evolution of the mammalian type of atlanto-axial rotation involves i) development of a dens, or odontoid process, and transverse, apical and alar ligaments, ii) loss of atlanto-axial zygapophyses, and iii) enlargement of the atlanto-axial intervertebral foramen. The dens is not the exact homologue of the atlas centrum as is generally believed. The dens is a neomorphic addition to the atlas centrum and reinforces, together with its associated ligaments, the altanto-axial joint, acting as a functional substitute for the lost atlanto-axial zygapophyses. Zygapophyses tend to restrict intervertebral rotation and are lost at the mammalian atlanto-axial joint which is specialized for rotation. The enlargement of the atlanto-axial intervertebral foramen is related to the specialization of the atlanto-axial joint for rotation and the necessity for preventing occlusion of the traversing neurovascular structures during rotation. Cyno-

donts possess an incipient dens, reduced atlanto-axial zygapophyses, and an enlarged atlanto-axial intervertebral foramen. It is likely that cynodonts had acquired at least a limited ability to rotate the atlas and head on the axis.

4) The vertebral count of *Thrinaxodon* is seven cervicals, thirteen thoracics, seven lumbars, five sacrals and at least five caudals. In *Cynognathus* the count is the same except that there are fifteen thoracic vertebrae. The cervical series, already seven as in most mammals, is moderately well differentiated from the thoracic. The thoracic series is differentiated from the lumbar on the basis of rib morphology; otherwise the differences are gradational and are relatively small. In *Thrinaxodon*, at least, all thoracolumbar vertebrae posterior to the fourth thoracic bear anteroposteriorly elongate neural spines; the anterior edge of each spine is received in a vertical cleft in the posterior margin of the preceding spine. This arrangement restricted vertebral column extension and it is probable that cynodonts employed only a very moderate range of sagittal flexion and extension during locomotion, less than in most mammals. All vertebrae in *Thrinaxodon*, with the exception of the atlas and the posterior caudals, bear anapophyses. The five sacral vertebrae are not fused. The exact number of caudal vertebrae, not known in any cynodont, was probably small and hence cynodonts were comparatively short-tailed.

5) In *Thrinaxodon* all presacral ribs bear near the proximal end a flat, expanded costal plate which imbricates with adjacent costal plates. In the earliest known cynodonts no costal plates are present. In later forms such as *Cynognathus* costal plates are retained in the posterior thoracic and the lumbar regions and are lost or are vestigial elsewhere. Typically the lumbar and sacral ribs are fused to the vertebrae in those forms possessing costal plates. Costal plates served for the insertion of the ilio-costalis division of the epaxial musculature. The elaborate costal plates of the most advanced cynodonts were characterized by an interlocking device with two pairs of articular facets on each plate.

6) The imbrication of adjacent costal plates did not inhibit lateral flexure of the vertebral column. Costal plates may indicate an unusually well developed iliocostalis muscle system. Such an arrangement, with the ribs acting as lateral levers, would efficiently produce lateral flexure. The result would emphasize a reptilian, rather than a mammalian, mode of locomotion. It is certain that the imbrication of costal plates, whether of the galesaurid or advanced cynodont type, served to greatly strengthen the vertebral column. Functionally this may represent an early "experiment" in musculoskeletal adaptation to sustain a more characteristically mammalian posture with the trunk persistently held off the ground.

7) The cynodont shoulder girdle consists of a scapula, coracoid, procoracoid, clavicle and interclavicle. The coracoid has an elongate posterior process, as in monotremes, and is not so reduced as is commonly illustrated. The glenoid faced posterolaterally and slightly ventrally; the long axis of the scapular blade was inclined about 25° anteriorly.

8) Evolutionary modifications of the shoulder girdle during the reptilian-mammalian transition appear to have been related to changes in forelimb posture and con-

sequently in forelimb mechanics. In pelycosaurs, substantial compressive force on the thorax was generated by the posture of a laterally-directed, horizontally-held humerus. This force was accommodated by a large scapulocoracoid plate and robust clavicles. In cynodonts the humerus was held at an angle of about 45° to the longitudinal body axis; its distal end was somewhat depressed relative to the proximal end. As a consequence compressive force on the thorax was reduced, and so was the relative size of the scapulocoracoid plate and clavicles. The lateral bowing of the cynodont scapula probably oriented the serratus musculature in a manner which offset much of the residual compressive forces.

9) In pelycosaurs the screw-shaped glenoid provided a set trackway which predetermined humeral excursion during all phases of locomotion. Such a mechanism is perhaps indicative of a primitive state of neuromuscular coordination. Humeral excursion primarily involved anteroposterior movement in an essentially horizontal plane, plus rotation about the long axis of the humerus. In cynodonts no vestige of the primitive screw-shaped glenoid remained. Much of the propulsive thrust was transmitted to the scapula as in mammals. Anteroposterior movement of the humerus involved a significant amount of depression and elevation of the distal end, thus presaging the mammalian condition. It is likely that some longitudinal rotation, a primitive characteristic, was retained.

10) The cynodont forelimb is robust, a feature that results as much from the comparatively large size of the head as from the forelimb's "primitive" morphology. In normal stance, the radius crossed over the distal end of the ulna from lateral to medial side, as in the mammalian position of pronation.

11) There are eleven carpals in *Thrinaxodon*, the only cynodont for which a complete carpus is adequately known. The digital formula of *Thrinaxodon* is 2-3-4-4-3, with a disc-like, vestigial phalanx in digits III and IV; it is probable that later cynodonts had a mammalian count of 2-3-3-3-3. In *Diademodon*, at least, the forefoot is substantially larger than the hindfoot.

12) The cynodont pelvis shows a number of major modifications of the pelycosaurian pattern. The anterodorsal expansion of the iliac blade is unquestionably related to the growth and reorientation of the gluteal musculature which, as Romer (1922b) suggested, approximates a mammalian condition; moreover, the increase in iliac blade length allowed the sacrum to include five vertebrae and thereby form a stronger sacroiliac articulation. The pubis is considerably shorter than in pelycosaurs but otherwise retains a pelycosaurian pattern. There is no evidence that cynodonts possessed separate prepubic ("marsupial") bones. A large obturator foramen of mammalian proportions is developed. The acetabulum is better ossified than in pelycosaurs and approximates a mammalian morphology in its socket-like shape and slightly ventral orientation.

13) In larger cynodonts the femoral head is well ossified, bulbous and reflected mediodorsally. The tibial facets on the distal end of the femur are neither parallel to the femoral axis as in pelycosaurs nor arranged in pulley-like fashion across the distal

end as in mammals; instead they are planar and lie at angles of about 45° to the femoral axis. This condition appears to be intermediate but depending on the disposition of the overlying cartilage may have closely resembled the mammalian pattern which permits a large degree of flexion and extension.

14) Consideration of the articular relationships on the hindlimb shows cynodonts to be intermediate between pelycosaurs and generalized mammals with regard to femoral posture. In pelycosaurs the femoral axis makes about an 80° angle with the body in normal stance; the distal end of the femur is slightly elevated relative to the proximal end. In cynodonts the same angle is about 55° compared with 25° in generalized mammals; the distal end of the cynodont femur is held below the level of the acetabulum but not as far ventrally as in mammals.

15) The origin of the mammalian lesser trochanter is reviewed with reference to the theories of Romer (1924) and Parrington (1961). Romer held that the trochanter on the anteroventral aspect of pelycosaur and therapsid femora is not homologous with the mammalian lesser trochanter because non-homologous muscles attach to each. Parrington concluded that the cynodont anteroventral trochanter is homologous with the mammalian lesser trochanter, although the pelycosaur trochanter in the same position is not. Parrington believed with Romer that the reptilian internal trochanter migrated posteriorly in the mammalian lineage and was lost; it was purportedly replaced by the lesser trochanter which migrated ventrally to assume the position of the displaced internal trochanter. The evidence for trochanter migration is questionable. It is here proposed that: i) there has been only one anteroventral trochanter in synapsids on or close to the line of mammalian ancestry; ii) a slight shift in muscle insertion accounts for the fact that non-homologous muscles insert on this trochanter in living reptiles and mammals; iii) the mammalian pattern of muscle insertion is functionally related to the repositioning of the hindlimb.

16) The plantigrade cynodont pes possesses numerous features well advanced toward a mammalian pattern. The sustentaculum tali and tuber calcis are large. The astragalus was at least as much supported by the calcaneum as by its own plantar contact, presaging the mammalian condition in which the astragalus lies entirely upon the calcaneum. The two separate calcaneo-astragalar facets are aligned obliquely to the calcaneal axis, a condition intermediate between that of pelycosaurs, in which they are parallel, and that of mammals, in which they are nearly transverse. The wedge-shaped cuneiforms and cuboid of cynodonts are evidence of the development of a mammalian type of transverse arch. The cynodont foot was relatively narrow and possessed complex intermetacarpal articulations, as in mammals. The phalangeal formula, of advanced cynodonts at least, is 2-3-3-3-3. Comparison of the pes of *Bauria* with that of an advanced cynodont shows that the latter is more advanced toward a mammalian pedal morphology than the former.

17) The less complete ossification in the appendicular skeleton of smaller cynodont genera creates apparent differences in morphology when compared to the better ossified limb bones of larger genera. If allowances are made for this fact, then it is clear

that the postcranial skeleton of cynodonts is remarkably uniform in morphology. Only in rib design do cynodonts display the tendency toward rapid evolutionary change in the postcranial skeleton.

18) There is no osteological evidence as yet that cynodonts possessed a diaphragm as suggested by Brink (1954, 1955, 1956). Moreover, there is no evidence of bony epiphyses. It is certain that cynodonts did not possess bony epiphyses but the question of a diaphragm cannot be settled either way with known material.

19) In details of morphology and function, the cynodont postcranial skeleton should be regarded as neither "reptilian" nor "mammalian" but as transitional between the two classes. It is inappropriate to conceive of cynodonts as representing a prototherian level of organization, for in many ways the monotreme postcranial skeleton is highly specialized. If indeed a cynodont is the common ancestor of all living mammals, then it is appropriate to examine the monotreme skeleton for cynodont characteristics, not vice versa.

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